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The structure of pelagic seabird assemblages in the African sector of the Southern Ocean

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This thesis is dedicated to my family: Monty, Penny, Doug, Joyce, Jayne, Jim, Josh, Marilyn and Amber.

1. Abstract

This study investigated the potential usefulness of aerial seabirds as indicators of the distribution of peculiar oceanic biotopes and prey populations in the African sector of the Southern Ocean. The hypothesis examined was that the distribution and abundance of seabirds are non-random and predictable with respect to the availability of prey at the sea-surface. The distribution of seabirds was correlated with prey density, in cases where the appropriate information was available. More often than not, however, data on prey distributions were unavailable, so that seabird distribution was correlated with the abiotic indicators of hydrodynamic processes which order the distribution of potential prey.

The distribution of seabirds was determined by means of shipboard observations. The trophic structure of seabird assemblages was assessed according to the diversity, biomass and abundance of 35 seabird species according to four principal diet-classes. The ecological structure of seabird populations was defined in terms of relationships between the trophic structure of seabird assemblages and Southern Ocean oceanography, meteorology and biogeography. The predictability of seabird distribution and abundance with respect to environmental variation was assessed using linear and nonlinear regression procedures. A deterministic model was developed in which analytical techniques are standardized and which can be applied to other ocean areas.

There are predictable associations between the trophic structure of seabird assemblages and the structure of the surface of the

sea. Assemblages of putative prey feature squid and fish in low latitudes, and plankton predominate in higher latitudes. The ecological structure of seabird populations reflects this trend on a macro-scale level. On a meso-scale level, the abundance of seabirds by diet-class correlates with the relative abundance of putative prey. Moreover, seabird abundance and biomass correlate positively with abiotic indicators of frontal zones and sea-surface mixing, where prey diversity and abundance are greatest. Regressions of seabird abundance with sea-surface temperature explain important aspects of the variation in the ecological structure of selected seabird populations.

This study showed that it may be possible to track the distribution of prey stocks through concurrent observations of seabirds and hydrography. Consequently, the descriptive model developed in this study contributes towards the objective of circumventing the need for direct sampling of prey stocks. The predictability of seabird distribution and abundance previously obtained has been surpassed by the results of this study through progressive reduction of the spatio-temporal scale of data collection and analysis, and by treating biotic-abiotic relationships with non-linear regression models where appropriate. The study concludes that sufficient advances have been made to justify further research into the use of selected species of aerial seabirds as indicators of prey distribution and abundance at sea.

2. Introduction

2.1. Rationale

The Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) sets out a policy for harvesting living resources in the Southern Ocean which is based on maintenance of the basic structure and dynamics of the constituent ecosystems (Hammond, 1982). The size of the Southern Ocean precludes the monitoring of every species which might be impacted by harvesting. Hence, it is intended that selected predatory species of the commercially important prey stocks (e.g. krill (Euphausiacea), squid and fish) be monitored, as part of a long-term management programme (Hammond, 1982). Aerial seabirds are candidates for such monitoring, because they are widely ranging, highly visible, top predators in the short marine food chains of the Southern Ocean. This study investigates if, and to what extent, seabirds are useful as indicators of the distribution and abundance of prey stocks in the African sector of the Southern Ocean.

The monitoring of seabirds as indicators for ecosystem management requires that a distinction be made between their breeding and non-breeding phases. Cody (1974) reported that polar seabird species take advantage of summer 'pulses' in biological production to maximize reproductive success. He suggested that this leads to 'communities' being structured largely as a consequence of

interspecific competition. The scarcity of breeding platforms for seabirds and seals in the Southern Ocean results in the concentration of these predators within relatively limited areas (Croxall, 1984). Seabirds breeding in the summer in the Southern Ocean tend to disperse at the end of the breeding season towards lower latitudes where zooplankton, squid and fish availability are not curtailed by winter conditions (Croxall, 1984). If interspecific competition for food among non-breeding seabirds is minimized by their dispersion over a range which is much broader than their breeding range, then their pelagic distribution is probably related directly to food availability.

If the distribution at sea of non-breeding aerial seabirds is determined primarily by the availability of food, then these animals could be useful as indicators of the distribution and abundance of their prey. Odum (1971) and Krebs (1972) suggest that the distribution and abundance of an indicator species should be limited by, or correlated with, the factor (e.g. prey availability) being monitored. The hypothesis that assemblages of non-breeding seabirds are organized principally by the availability of food would be supported by showing that: 1. non-breeding seabird dispersion is non-random; 2. the trophic structure of aerial seabird assemblages at sea is consistently the most important dimension ordering the avifauna; and 3. the trophic structure of aerial seabird assemblages correlates with the distribution of their prey (see Section 4. for definitions of terms).

Rough seas, weather and limited dedicated ship-time hamper studies of the diets of seabirds at sea, so that information directly linking birds and prey is extremely expensive to obtain and very

slow to accumulate (Siegfried, 1985). Therefore, associations between seabirds and the biological and physical processes which concentrate, or otherwise, make food available to them at the sea-surface is, at present, the best approach available for correlating their distribution with their prey (Kinder et al., 1983). If, in the Southern Ocean, the trophic structure of seabird assemblages is predictable with respect to the habitat structure, then it is realistic to use seabirds as indicators in an ecosystem model.

1.1. Objectives

The objectives of this study are aimed at determining how, if at all, seabirds can be used as indicators of the distribution and relative abundance of prey stocks or peculiar oceanic biotopes which concentrate prey species. More particularly, I attempt to:

1. Describe the distribution and abundance of seabirds at sea in the African sector (see below) of the Southern Ocean.

2. Identify and rank the environmental correlates of seabird dispersion at sea.

3. Relate pelagic seabird distribution to prey availability near the sea-surface where this is practicable.

4. Determine the relationship of seabird distribution at sea with selected environmental correlates, and establish the suitability of pelagic seabirds as indicators of hydrographic conditions which influence the distribution of potential prey species in the Southern Ocean.

2.3. Presentation of dissertation

The objectives were approached by exploring a sequence of hypotheses on the macro- and meso-scales of spatio-temporal distribution:

1. The distribution of non-breeding aerial seabirds at sea is non-random.

2. Non-breeding aerial seabirds are organized at sea into assemblages which reflect the biogeography of the marine flora and fauna.

3. Changes in the structure of aerial seabird assemblages at sea correlate with changes in the physical structure of the marine habitat (e.g. sea-surface temperature or air-sea interface characteristics) and, in particular, with physical processes which concentrate or otherwise influence the availability of food to seabirds.

2.3.1. Macro-scale patterns of seabird distribution

The first hypothesis was examined by mapping (Southern Ocean Pelagic Seabird mapping program (SOPS), Abrams et al., 1981) seabird species richness, species diversity and abundance of individuals for all species observed during 12 research and supply cruises of the M. V. S. A. Agulhas in 1979-1981. Annual composite patterns were assessed for the Africa-Antarctica environmental

gradient from two complete field seasons. These results are reported in Section 5.1.1.

The second hypothesis was assessed by exploring the ecological structure of seabird assemblages at sea in terms of the relative proportions of secondary to tertiary consumers along the Africa-Antarctica environmental gradient. Accordingly, the macro-scale environmental gradient was characterized as a meridional series of habitat-type zones. The annual energy and food requirements of the seabird assemblages observed in each zone were calculated to determine if the changes in the ecological structure of seabird assemblages along the environmental gradient are those which can be expected from information available on the biogeography of plankton, squid and fish in the Southern Ocean (Section 5.1.1).

The third hypothesis was examined through bivariate and multivariate linear regression procedures (Dixon, 1981, 1982 BMDP statistical software), which were used to identify those environmental parameters which covary with seabird parameters (Section 5.1.2). The strength and nature of these associations were then explored in a non-linear regression model (Section 5.1.2) and by means of correspondence analysis (a descriptive ordination procedure (Greenacre, 1984; Section 5.1.3)).

2.3.2. Meso-scale patterns of seabird distribution

The resolution of the three hypotheses at a macro-scale showed that the variance in seabird abundance was not fully explained by correlation with linear environmental gradients. Moreover, examples of meso-scale variations, nested within macro-scale patterns, occurred in the assessment of hypothesis 3. Subsequently, through a refinement of the spatio-temporal scale in both data collection and analysis, I clarified relationships which were masked by the lumping of data.

The three hypotheses were re-examined using data sets on seabird distribution, certain prey distributions and physical oceanographic features at a meso-scale level. I report three regional studies (Sections 5.2.1, 5.2.2 and 5.2.4) which address the first hypothesis. Here, I draw attention to the first of these which is a good example of the non-random distribution of seabirds in a deep-sea area.

The first hypothesis was re-examined by determining the distribution of seabirds in an area which, from a macro-scale perspective, is a zone of high seabird abundance (Section 5.2.1). The second hypothesis was addressed from a meso-scale perspective by relating hydrographic and hydro-acoustic surveys to seabird distribution. Hydro-acoustic surveys are employed by fisheries biologists to assess the distribution and abundance of plankton (including krill) and fish stocks. In two studies (Sections 5.2.2, 5.2.3), I assessed the co-occurrence, at meso-scale sea-surface features, of seabirds with krill, and seabirds with zooplankton; the distribution of these prey were represented by hydro-acoustic data.

The third hypothesis was examined by relating real-time oceanographic and seabird data (Section 5.2.4). I report how the seabird assemblages associated with each type of meso-scale sea-surface feature (e.g. fronts, eddies) differ from each other. The hydro-acoustic and hydrographic surveys of Sections 5.2.2 and 5.2.3 did not produce data on a fine enough scale to permit statistical correlation with seabird abundance. Fortunately, the types of meso-scale features (e.g. fronts, eddies) found in the hydrographic and hydro-acoustic studies were represented in Section 5.2.4, so that statistical correlations between seabirds and these meso-scale features are tested fully in this section. Hence, I was able to determine if the reduction of spatio-temporal scale of analysis improves the correlation coefficients derived from seabird-habitat relationships.

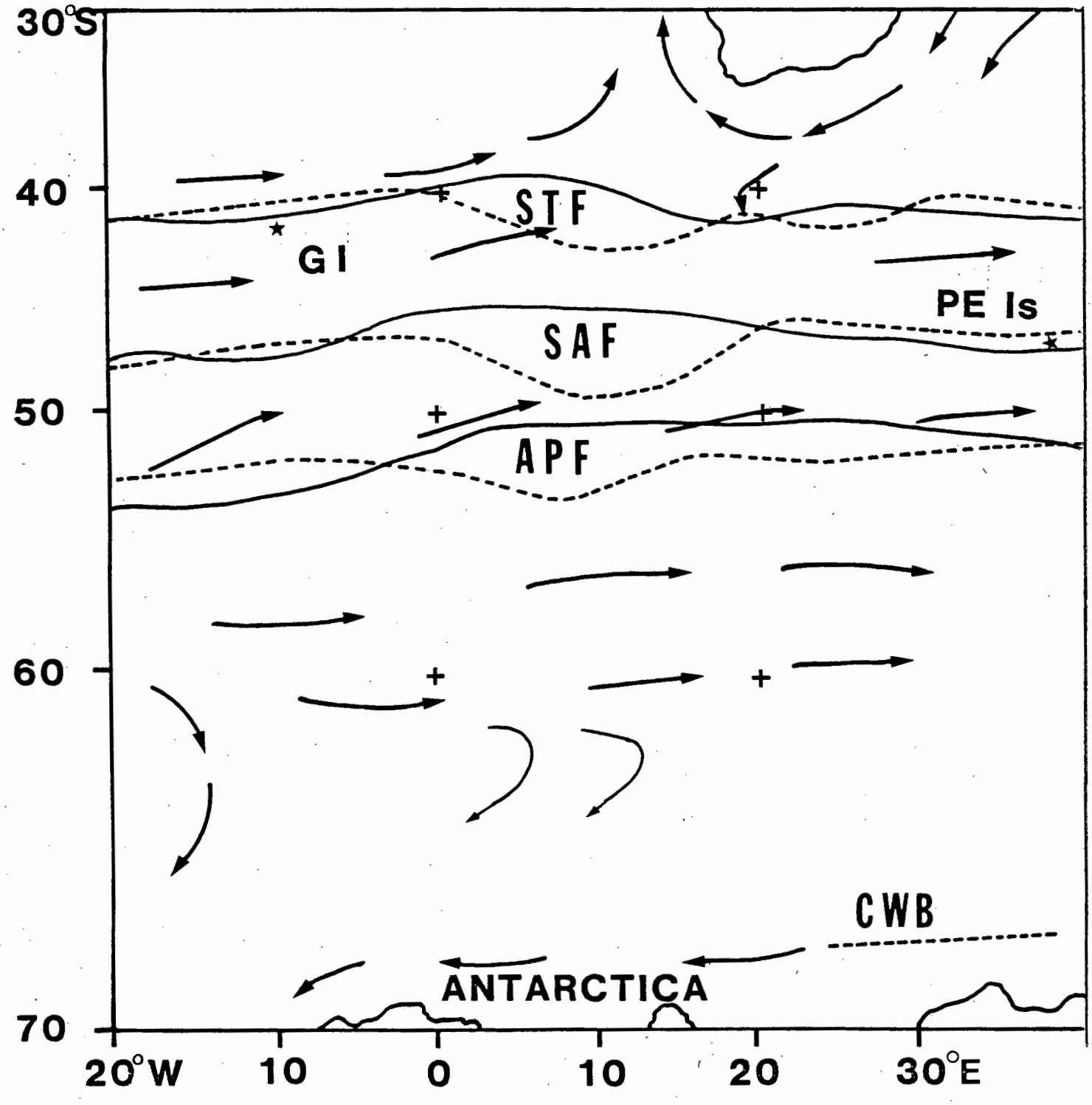
This thesis consists of seven published or submitted papers which relate to one or more of the objectives and hypotheses listed. This format has been used because I have attempted to communicate my findings as quickly as possible. Hence, there is some unavoidable repetition of information. The Synthesis (Section 6.) will, I hope, facilitate the readers' efforts to comprehend rapidly the theme of the study. References applicable to each sub-section of the Results (Section 5.) appear with that sub-section, and references applicable to the Synthesis and Introduction are presented at the end of their respective sections.

location and nature of the 'Antarctic Divergence'. The details of the Weddell Gyre and its interface with the 'East Wind Drift' are now for the first time being studied in winter (Gordon and Huber, in press). Whitworth (1980) and Nowlin and Clifford (1982) have named a frontal feature close to Antarctica as the 'Continental Water Boundary'.

The interface zone between the Antarctic Circumpolar Current and the sub-tropical seas (i.e. the Agulhas Current and the Benguela Current regions south of Africa) is perhaps the most complicated biogeographical boundary zone in the Southern Ocean (Lutjeharms, 1981; Gordon, in press). My thesis includes data from the most detailed, intensive oceanographic research in the area: the Agulhas Retroflection Cruise (Gordon, in press). It is not clear whether this area includes a convergence, although a series of thermohaline fronts exists and the latitudinal separation of these fronts varies considerably (Lutjeharms and Valentine in press).

There is consensus that frontal zones are sites of high nutrient concentration and biological production and diversity (Emery et al., 1974; Holm-Hansen et al., 1977; Deacon, 1982; Tranter, 1982; Weber and El-Sayed, 1985). The flora and fauna of each major biogeographic zone mix within the frontal zones and a variety of physical processes mix nutrients and organisms across the fronts at irregular intervals (Peterson et al., 1982; Tranter et al., 1983a). Accordingly, the recent attention of biological oceanographers to finer scales of data resolution has revealed that the diversity and abundance of pelagic zooplankton and squid are enhanced in the vicinity of meso-scale mixing processes (Brandt, 1983; Tranter et al., 1983 a, b).

Figure 1. The African sector of the Southern Ocean showing prevailing current flow (arrows), mean summer (dashed lines) and winter (continuous lines) positions for the Sub-tropical Frontal zone (STF), the Sub-Antarctic Frontal zone (SAF), the Antarctic Polar Frontal zone (APF) and the position of the Continental Water Boundary (CWB). The locations of Gough Island and the Prince Edward Islands are also indicated.



4. Methods

The best examples of the use of multivariate analyses of the ecological structure of avian communities in relation to habitats come from terrestrial studies. Wiens and Rotenberry (1981) characterized and ranked some of the structural dimensions of terrestrial bird communities, using the correlations of selected environmental parameters with the occurrence in time and space of the birds. Wiens and Rotenberry (1981) point out that if a relationship exists between birds and their habitat, then where environmental conditions change, there should be consistent and interpretable changes in the occurrence of species. Wiens and Rotenberry (1981) found low correlation coefficients for their bird-habitat study, which they acknowledged could be due to inappropriate spatial scale of resolution in the data. Meents et al. (1983) were able to explain relatively higher percentages of the variance in terrestrial bird abundance by treating biotic-abiotic associations as non-linear.

Wiens and Rotenberry (1981) advise that in the analysis of ecological factors affecting animal distributions, the potentially confusing effects of evolution and biogeography may be minimized by considering community composition and dynamics at 'more local scales'. Thus, by considering my data on seabird populations as assemblages, I resolved the dynamics of their distribution rather than trying to fit them into communities (see below). As per Wiens and Rotenberry (1981) and Meents et al. (1983), I used regression-based statistics to characterize and compare the seabird assemblages of selected spatio-temporal scales, in order to identify the relative importance of their biotic and

biotic-abiotic associations.

I used two techniques for characterizing differences in seabird diversity and abundance from one area to another: 1) species or species-group correlation matrices, and 2) univariate and multivariate correlations between selected seabird variables and environmental variables. Technique 1 was used as a 'signature' for particular seabird assemblages in comparisons between the avifaunas of discrete habitat areas or oceanic zones. Technique 2 was used to correlate gradual or sudden changes in seabird diversity and abundance with gradual or sudden changes in the physical parameters representing environmental features or gradients. The focus of technique 2 is the environmental processes which make prey available to the seabirds. These two techniques together described a model of the ecological structure of pelagic seabird assemblages. The applications of these techniques to each data set are detailed in each section of the results of the thesis.

The biases inherent in counts of seabirds at sea (Griffiths, 1981) necessitated using data from one vessel-type, collected by a limited number of observers using an internationally accepted field method (Seabird Mapping Scheme, 10-minute card method, Anon., 1982). In order to minimize the biases inherent in counts of birds at sea, inter-observer bias was minimized by using data from a minimum of observers. New observers were trained by current staff and their data verified in the field under supervision of the project leader and the current staff. Observations were suspended when a standard cut-off point in visibility was passed. A narrow field of view (beam-bar) and a fixed distance from the ship were used to minimize recounting of individual birds, which I

consider to be the most serious potential bias in counts of birds at sea. Penguins were omitted from this study, because they are difficult to observe and count from ships at sea.

The sampling procedure was to collect as many counts in series as possible during daylight, ensuring that these were always in one hour blocks at the least. This provided steaming transects of 25 km or more. Although it is most desirable that each field count be a random sample, this condition was only approximated because data from a steaming ship are a time-series of counts. These data do not conform strictly to the assumption of random sampling inherent in the use of regression-based models. Therefore, the results of correlation analyses do not, in this context, offer a true measure of predictability because some of the 'explained variance' could be due to autocorrelation. It is for this reason that the thesis presents two methods of examining correlations between seabirds and physical parameters. Correlation matrices were used to highlight relationships for further analysis. Such statistics usually require the assumption of random sampling, but here were used as relative measures of association. The second method, bivariate or multivariate regression, addressed the variation in bird numbers along environmental gradients. The thesis draws from linear regression procedures the most important environmental determinants of seabird distribution. Although these statistics are not absolute measures of variance explained, the bias is the same for all environmental parameters, so that these regression procedures helped to identify the physial parameter most strongly associated with variance in seabird parameters: sea-surface temperature. Thereafter, a curvilinear model was used which reflects graphically the autocorrelation in seabird counts as the natural, gradual increase up to and decrease away from an

oceanic feature of attraction, i.e. SST fronts. The curvilinear approach is new to the analysis of seabird distribution and is superior to linearizing curves because the output provides a graphical presentation of the raw data, the theoretical curve, a measure of the fit and an indication of the SST characeristics of the front. This approach is the most meaningful to those familiar with pelagic seabird research.

In using linear regression procedures for the statistical correlation of seabird-habitat relationships, I generally transformed the raw seabird counts to normalize the distributions which are skewed by a large number of zero counts. This transformation (y=log(x+1)) reduced the influence of zero counts and of especially large counts. This makes my analyses comparable to a rank correlation approach, and I recognize that the regression equations produce measures of association which are approximate, i.e. the predictive values of my results are relative, not absolute. The variance explained in my non-linear model (Sections 5.1.2 and 5.2.4), is not absolute, which is why I supported the model's results with an analysis of variance to determine if the variance explained by my model is significantly greater that the variance explained by a randomized model (Section 5.2.4).

Seabird counts were coded and entered into a Sperry-Univac 1100 computer, including with each 10-minute observation the numbers of all species sighted in a fixed area and all the environmental parameters available for that 10-minute period from the ships' continuous and non-continuous recorders.

The selection of data subsets for each study differed. Sections 5.1.1 and 5.1.2 included two complete field seasons. In each year

there were approximately the same number of field observations (3005 and 2918, 1979-80 and 1980-81, respectively) from a replicated cruise schedule. This ensured that no habitat zone had less than 250 observations and that all oceanic fronts were crossed in all months, except for the Antarctic Polar Front in winter. Further, all cell-area means were derived from a minimum of 6 observations in each calendar season (or in cases of peripheral cell areas, the adjacent cells were fully sampled). Moreover, all habitat features (e.g. fronts) were sampled by at least 6 crossings, which included not less than 25 observations. The annual composite data in Sections 5.1.1 and 5.1.2 were the same except that for the multivariate biotic-abiotic analyses, 45 cases were dropped from Section 5.1.2 due to missing values for some abiotic parameters and two additional cruises were included in the analysis of cruise tracks across fronts. Section 5.1.3 assessed the single cruise track which best represented the complete study area environmental gradient. This cruise was the most intensive summer cruise for which reliable oceanographic data were available.

Sections 5.2.1 and 5.2.3 examined a deep-sea area important to the study of krill ecology and included hydrographic data not normally available over an intensive grid. Section 5.2.2 examined a deep-sea frontal zone in conjunction with a sub-Antarctic seabird breeding site, and included extensive hydrography and hydro-acoustics over an intensive grid. Such extensive multidisciplinary studies of areas which contain meso-scale hydrographic phenomena merited isolation for special analysis. The research cruise which provided the data for Section 5.2.4 was the culmination of a trend among oceanographers to resolve meso-scale hydrography in and near a major deep-sea frontal zone,

and as such provided the best data set for the purposes of this thesis.

The diet-classes into which seabirds species have been lumped for analyses in this thesis were derived from studies conducted primarily at or near breeding sites. It was not logistically possible to confirm these classifications at sea while the distributional data were collected. The classification of seabirds by diet for this thesis was based upon the literature (see relevant Sections below) and unpublished data. Unpublished information which was more relevant to the African sector of the Southern Ocean superseded published data. This compromise approach was facilitated through BIOMASS participants who have agreed upon the classification used in order to permit international collaboration on seabird at sea data analysis.

The seabird diet classes presented in Section 5.1.1 and throughout the thesis reflect this approach. It is important to point out that where the problem of diet-shifting among seabirds might have interefered with the interpretation of the results in this thesis, the analysis and discussion accounts for this. In all cases the single species data comprising the diet classes are presented in Appendices. Where relevent, the species most important to a specific interpretation were analysed independently of the diet classes. In none of these cases did the results of single species analysed independently of the diet classifications contradict the results or interpretation of the species lumped by diet class.

In analyses performed as background to this thesis, the co-occurrence of seabird species was assessed to show the difference between the *a priori* classification used herein and a *post priori* classification of species by geographical

co-occurrence. The seabird distribution data used for this analysis was that of the first two seasons (i.e. 1979/1980-1980/1981, the data sets for Sections 5.1.1-5.1.2). The data were analysed according to the oceanographic zones identified in Section 5.1.1. A cluster analysis was performed on seabird variables (single species) based on presence/absence to minimize dependency upon absolute counts (G.L. Hunt, pers. comm.), which provided a measure of association between species occurring within one 10-minute field observation. The data for the sub-tropical and sub-Antarctic zones were used because sampling south of 50°S was severely biased by season (i.e. summer only).

In all five zones, a strong association occurred between the most abundant planktivore (i.e. prions Pachyptila or Blue petrels Halobaena caerulea) and either a mixed-diet species (Soft-plumaged petrel Pterodroma mollis or Kerguelen petrel Pterodroma brevirostris) or a squid-eater (Fulmar Fulmarus glacialoides). In most zones a pair of diads or triads of these species occurred independently of each other. In sub-tropical zones, clusters included all of the above species as well as a variety of species from all four diet-classes, and these broad clusters were segregated from Giant petrels Macronectes or planktivores (e.g. Phalaropes). In sub-Antarctic zones, the diads and triads noted above segregated from smaller clusters which represented cross sections of the diet-classes (e.g. Black-browed albatross Diomedea melanophris with Atlantic petrel Pterodroma incerta; skuas Catharacta with Yellow-nosed albatross Diomedea chlorohynchos; Sooty shearwater Puffinus griseus with Whiteheaded petrel Pterodroma lessoni).

The cluster analyses showed generally weak clustering by species.

This reflects the trend throughout the thesis that all seabird species are attracted to frontal zones. Within frontal zones, where many of the birds are likely to be searching for food, it is not surprising to find clusters which represent predator assemblages which potentially take a cross-section of the food-chain. This result strengthens the point of the thesis which holds that the distribution and abundance of seabirds at sea is most strongly influenced by the structure of the marine habitat. This point is underscored in two ways by the cluster analysis results.

In the SAF zone there is a cluster of near-island species, including all of the penguins and skuas and albatrosses. In the STC, a frontal zone known for high biological productivity and seabird abundance, the clusters included the most species spanning the widest range of diets and feeding behaviours. In the higher latitudes (PFZ), strong clustering occurred among species known to take krill and zooplankton and which occur in large flocks randomly distributed over the very large, homogeneous habitat area.

Certain terms used in this thesis require definition. I avoid using the term 'community', because it implicitly or explicitly implies that a degree of interaction occurs between its components (Odum, 1971; Krebs, 1972). I define a seabird assemblage for a given area and time period by determining the percentage occurrence of each species or diet-class according to total abundance (i.e. numbers of individuals) and total biomass (assuming a mean live mass per individual per species). Thus, an assemblage is a collection of species in a space/time framework, as opposed to a collection of species for which some assumed link

exists. Comparisons between assemblages are made using mean values for species richness, diversity, abundances and biomass, per observation. Species richness is the number of species, and species diversity is the Shannon diversity index for a seabird assemblage. The trophic structure of an assemblage is characterized by the mean values of species richness, species diversity and the abundance (numbers of individuals) of seabirds ordered by principal diet-classes. Thus, trophic structure reflects the theoretical prey-type requirements of an assemblage. The ecological structure of the avifauna is defined by the relationship between the structure of a given physical habitat-type and the trophic structure of the seabirds present.

Habitat-types are defined in each instance by the oceanographic parameters which are available to distinguish between oceanic areas. Similarly, on a broader scale, biogeographic zones are identified by the latitudinal boundaries of major water masses. For the identification of habitat-types, or zones, I have relied on both consultation with oceanographers and on the data logged together with the seabird observations. For this thesis, macro-scale habitat areas are technically defined as areas greater than 500km diameter, but are practically defined as geographic zones (e.g. broad frontal zones which include seasonal variation). Meso-scale areas cannot be absolutely defined because their structure varies over weeks or months. Consequently, in this thesis, each meso-scale feature is specified and an approximate distance measure is sometimes provided, but this cannot be standardized.

For the biogeography of the Southern Ocean, I rely on Deacon (1982), Nowlin and Clifford (1982), Tranter (1982) and Clifford

(1983). Terminology, or names of currents and zones, come from the respective authors cited in each section of the results. Thermohaline fronts are generally considered in this thesis to be areas where currents, water masses or meso-scale features meet and there is a rapid change in sea-surface temperature and salinity. 'Convergences' and 'divergences' are not addressed specifically in analytical procedures in this thesis, because their oceanographic definitions are vague.

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5. Results

5.1. Macro-scale seabird distributions

Pelagic seabird distribution and abundance in relation to macro-scale structure of the African sector of the Southern Ocean

Seabird distributional data are used in this section to describe the way in which seabirds are organized into assemblages with respect to an Africa-Antarctica environmental gradient. Section 5.1.1 is a published paper which examines the latitudinal zonation of the seabirds over two years. This paper describes the trophic structure of seabird assemblages by the amount of energy theoretically required by the aerial avifauna observed in the study area. The proportions of carbon required by the birds in the forms of plankton, squid and fish are presented for the oceanographic habitat zones which represent the environmental gradient between Africa and Antarctica.

Section 5.1.2 is a published paper in which the macro-scale zonation of the avifauna is quantified in terms of selected oceanographic and meteorological determinants of seabird distribution and abundance. The resolution in these data of meso-scale hydrography was sufficient to develop the hypothesis that there is an important influence of meso-scale habitat

features on seabird distribution.

Section 5.1.3 is a manuscript presently under consideration for publication in a journal. The paper describes the non-linear relationship of seabird abundance with the Africa-Antarctica environmental gradient. The data include relatively intensive sampling of seabird, oceanographic and meteorological parameters. This section describes graphically the mathematical form of the curvilinear relationship between seabirds and their environment, which provides the basis for further non-linear analyses.

5.1.1. Energy and food requirements by region

Energy and food requirements of pelagic aerial seabirds in different regions of the African sector of the Southern Ocean

Summary. The African sector of the Southern Ocean includes 3 regions separated by oceanic fronts. The frontal areas between the sub-tropical, sub-Antarctic and Antarctic regions are characterized by relatively high nutrient and biotic production levels. In addition, the Benguela upwelling system over the southwestern African continental shelf is especially productive. Daily Energy Expenditures (DEE) of seabirds capable of flight were compared to see whether differences in primary productivity between different areas at sea are reflected at higher trophic levels. Theoretical carbon flux to seabirds at sea during 1979-1981 was calculated to be between 0.040 g C m^2 yr^{-1} and 0.224 g C m^2 yr^{-1}. The greatest C flux to seabirds occurred in the sub-tropical, and in certain frontal, areas.

Introduction

It has been suggested that seabirds could serve as indicators of the distribution of prey populations in the Southern Ocean, because they are the most visible carnivores at sea (Anon., 1977). High seabird abundance has been related to enhanced prey availability at oceanic fronts in the Bering Sea (Hunt et al., 1981; Schneider, 1983), and near Antarctica (Ainley and Jacobs, 1981). Aerial seabirds (species capable of flight) in the Southern Ocean are concentrated in convergence, divergence and frontal zones (Abrams and Griffiths, 1981; Ainley and Jacobs, 1981; Abrams, 1982; Griffiths et al., 1982). These zones are characterized by steep thermohaline gradients and high relative abundance of nutrients, plankton, squid and fish (El-Sayed, 1970; Holm-Hansen et al., 1977; Iverson, 1977; Hulley, 1981; Tranter, 1982).

In this paper I report the minimum amount of prey biomass required by aerial seabirds, based on their energy needs, in the African sector of the Southern Ocean during 1979-81. More particularly, the amount of carbon theoretically transferred through plankton (principally krill, Euphausiacea), squid and fish to aerial seabirds is compared between 9 oceanographic zones. The distribution of seabirds is discussed in the context of the physical processes which could influence the availability of prey. Comparisons are made of the C flux and food required by seabirds in the African sector of the Southern Ocean and other oceanic regions.

Methods

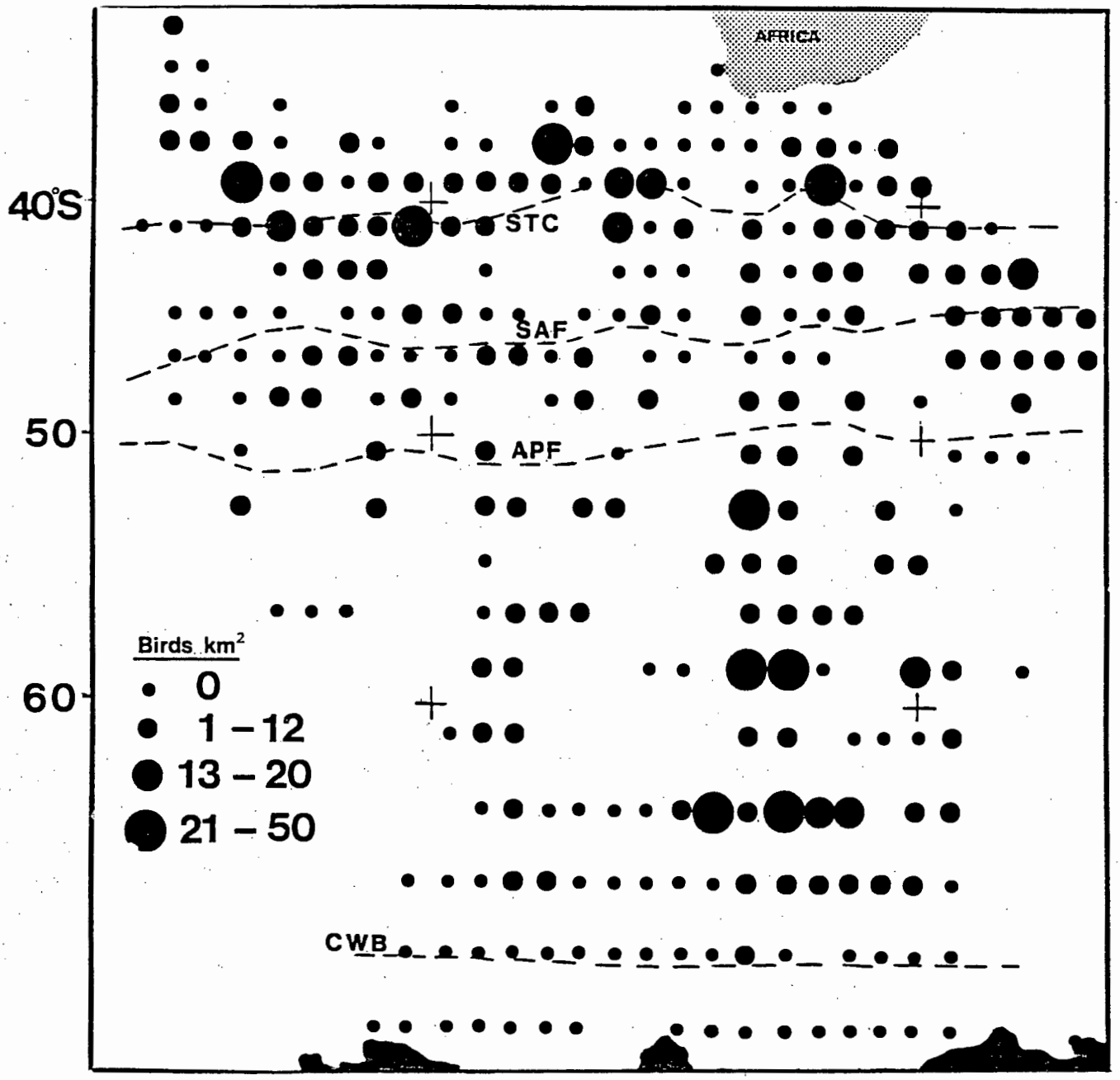
Seabirds (excluding penguins) were recorded during 12 separate

cruises of the M.V. S.A. Agulhas between April 1979 and June 1981 (Fig. 1). Similar areas were covered during the same seasons in 1979-80 and 1980-81. Attempts were made to count all birds observed flying past the moving ship (mean speed = 23.4 km h^{-1}) or sitting on the sea in a 1km-wide transect (abeam of the ship) during 5923 10-min (in 1h periods) observation sessions (Griffiths, 1981). No counts were made within 100 km of breeding sites of any species.

Seabird density estimates (no. birds km^{-2}) were calculated for 4 frontal zones and 5 zones between the fronts and continents (Fig. 1). The locations of fronts were taken from Deacon (1982) and Lutjeharms and Valentine (in press). The inter-frontal zones are named according to the fronts bordering the zones (i.e. Sub-tropical Zone (STZ) and Sub-tropical Convergence (STC); Sub-Antarctic Zone (SAZ) and Sub-Antarctic Front (SAF); Polar Frontal Zone (PFZ) and Antarctic Polar Front (APF); Antarctic Water Zone (AWZ) and Continental Water Boundary (CWB); Continental Water Zone (CWZ) and Antarctica). Mean mass per bird in plankton-, squid-, fish-, and mixed-diet classes was based on the proportionate abundance of each species which occurred in each of the 9 zones (Appendix 1).

Theoretical energy requirements (Daily Energy Expenditure) (DEE in kJ per bird of mean mass per day; Walsberg, 1980) were calculated for each diet class in each zone. The food (ww mass) of plankton- (including krill), and squid-eating birds was assumed to have an energy value of 4.51 kJ g^{-1} (Mauchline, 1980), and that of fish-eaters to be 21.0 Kj gdw^{-1} x 0.27 gdw/gww (Schneider and Hunt, 1982) Equal proportions of plankton, squid and fish were assigned to the mixed-diet species. All birds were assigned an

Fig. 1. Pelagic distribution (no. birds km^2) of planktivorous seabirds in the African sector of the Southern Ocean, 1979-1981. Approximate positions are given for the Sub-tropical Convergence (STC), Sub-Antarctic Front (SAF), Antarctic Polar Front (APF) and Continental Water Boundary (CWB)



assimilation efficiency of 80% (Clarke and Prince, 1981). Carbon flux was based on a value of 0.4 g C g^{-1} dw prey (Curl, 1962). The seabirds' requirements for the area north of the Antarctic Polar Front (maximum of 53°S) (Lutjeharms and Valentine, in press) were full-year composites, and south of the winter pack-ice limit half-year composites (Nov.- March), because aerial seabirds cannot forage in ice-covered seas.

The Daily Energy Expenditure (Walsberg, 1980) equations used here produced generally higher values than any of the formulae reviewed by Schneider and Hunt (1982). However, Weathers and Nagy (1980) found Walsberg's (1980) formula to be conservative, based on determinations of metabolic rate using labelled water turnover rates in free-living animals. Weathers and Nagy (1980) made the methodological comparison using a bird with an inordinately high water turnover rate, so that their D_2O^{18} method would perhaps slightly under-estimate actual metabolism. This reinforces the conservative bias of Walsberg's (1980) formula.

The Walsberg (1980) formula used was:

$$\log (DEE) = \log (13.64) + 0.663 \log (Mass\ g)$$

Results

The sub-tropical areas collectively supported the highest avian density (Fig. 1, Table 1); the birds being concentrated in the Sub-tropical Zone. In abundance, the avifauna was dominated by planktivores at the Sub-tropical Convergence and large-bodied squid-eaters nearer the African continent (Figs 1-2).

High abundance of large-bodied species in the north of the survey area was reflected as a maximum flux of C (0.181-0.224 g C $m^2 yr^{-1}$, Table 2, Fig. 3) to seabirds in the sub-tropical areas. The relative requirements of plankton-eaters increased in high latitudes (Fig. 3); the Antarctic Water Zone theoretically supporting, per unit time, a C flux (0.086 g C m^2 0.5 yr^{-1}) similar to those of the sub-tropical areas (Table 2). The avifauna of high latitudes contained a high abundance of relatively small-bodied birds adapted to utilizing patchy but locally rich prey concentrations typical of areas south of 50°S (Mauchline, 1980; Abrams, 1982; Tranter, 1982).

Large squid-eating albatrosses and petrels require 10-12 % of their DEE for flight (Table 3). To sustain continual flight, albatrosses require between 85 and 160 g squid daily. Thus, based on a meal of 650 g (Prince, 1980a), a relatively small albatross could forage for 6 d and a Wandering Albatross for 3 - 4 d before losing body mass. Prions, on the other hand, use daily 67 g food for flight alone, which is over 50 % of their DEE (Table 3). At 12 g per meal (Prince, 1980b), they require 5-6 meals d^{-1}, or a meal every 4-5 h, just for flight.

Fig. 2. Pelagic distribution (no. birds km^2) of squid-eating seabirds in the African sector of the Southern Ocean, 1979-1981. See Fig. 1 for explanation of abbreviations

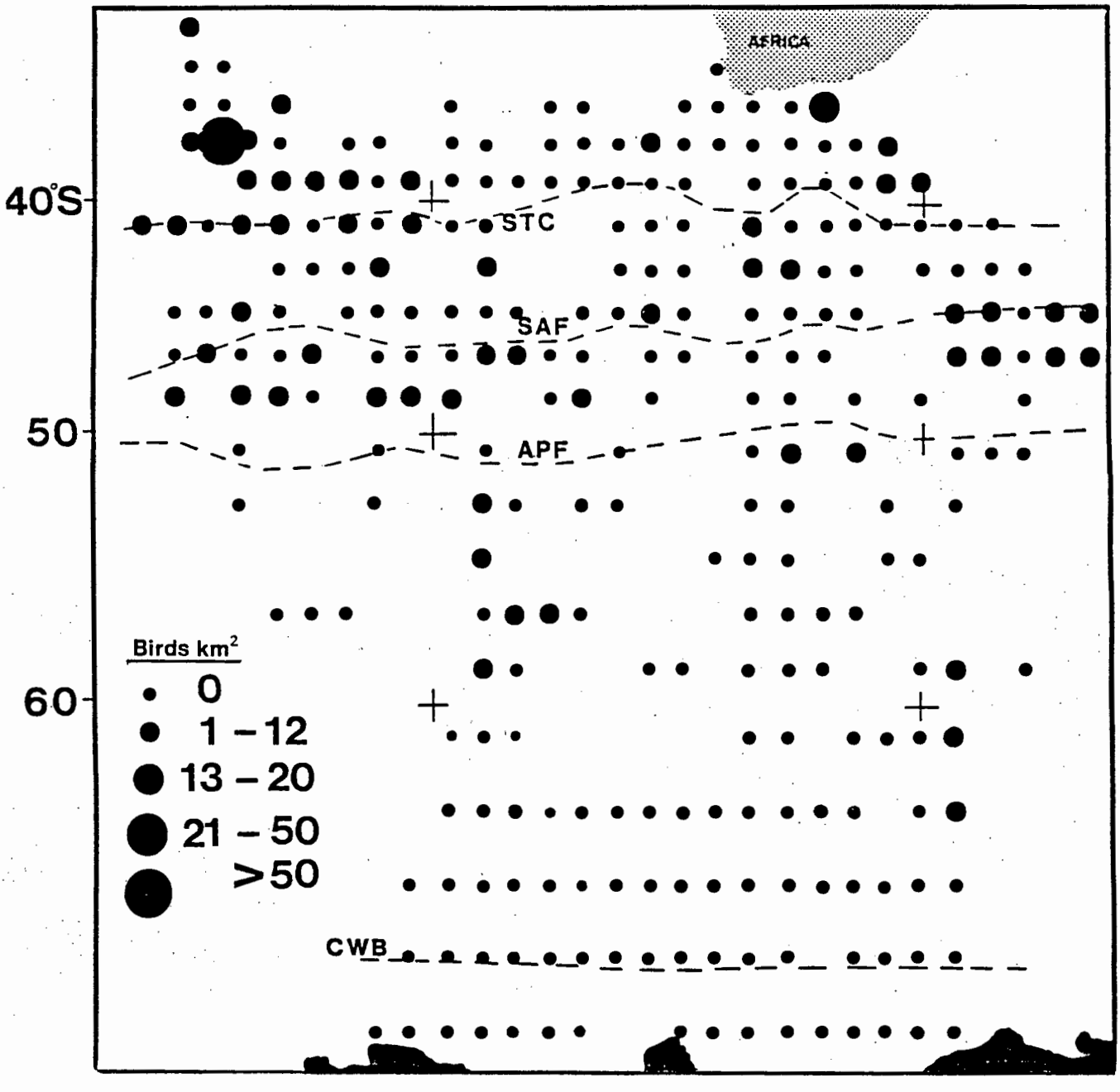


Table 1. Mean densities of seabirds (no. birds km^{-2}) and their energy requirements (Daily Energy Expenditure, Kj km^{-2}) in the African sector of the Southern Ocean, 1979-1981. Data for zones south of APF represent half-year composites. See text for names of zones

Zone	Diet class								No. of seabir counts
	Planktivores		Squid-Eaters		Piscivores		Mixed		
	Density	Energy	Density	Energy	Density	Energy	Density	Energy	
STZ	2.6	983	2.7	4 166	0.4	381	0.5	396	1 363
STC	4.0	1 503	1.3	2 575	0.3	209	1.1	864	865
SAZ	1.9	718	0.7	1 409	0.1	73	0.8	523	520
SAF	1.2	482	0.7	1 426	0.1	54	0.6	460	497
PFZ	1.9	721	0.5	1 158	0.1	30	1.1	730	255
APF	2.3	866	0.6	960	0.5	516	1.6	1 041	115
AWZ	7.0	2 838	0.5	852	0.4	449	1.8	1 315	661
CWB	2.6	1 113	0.2	348	0.7	718	1.0	944	1 224
CWZ	0.1	54	0.1	154	0.8	281	2.3	2 175	423

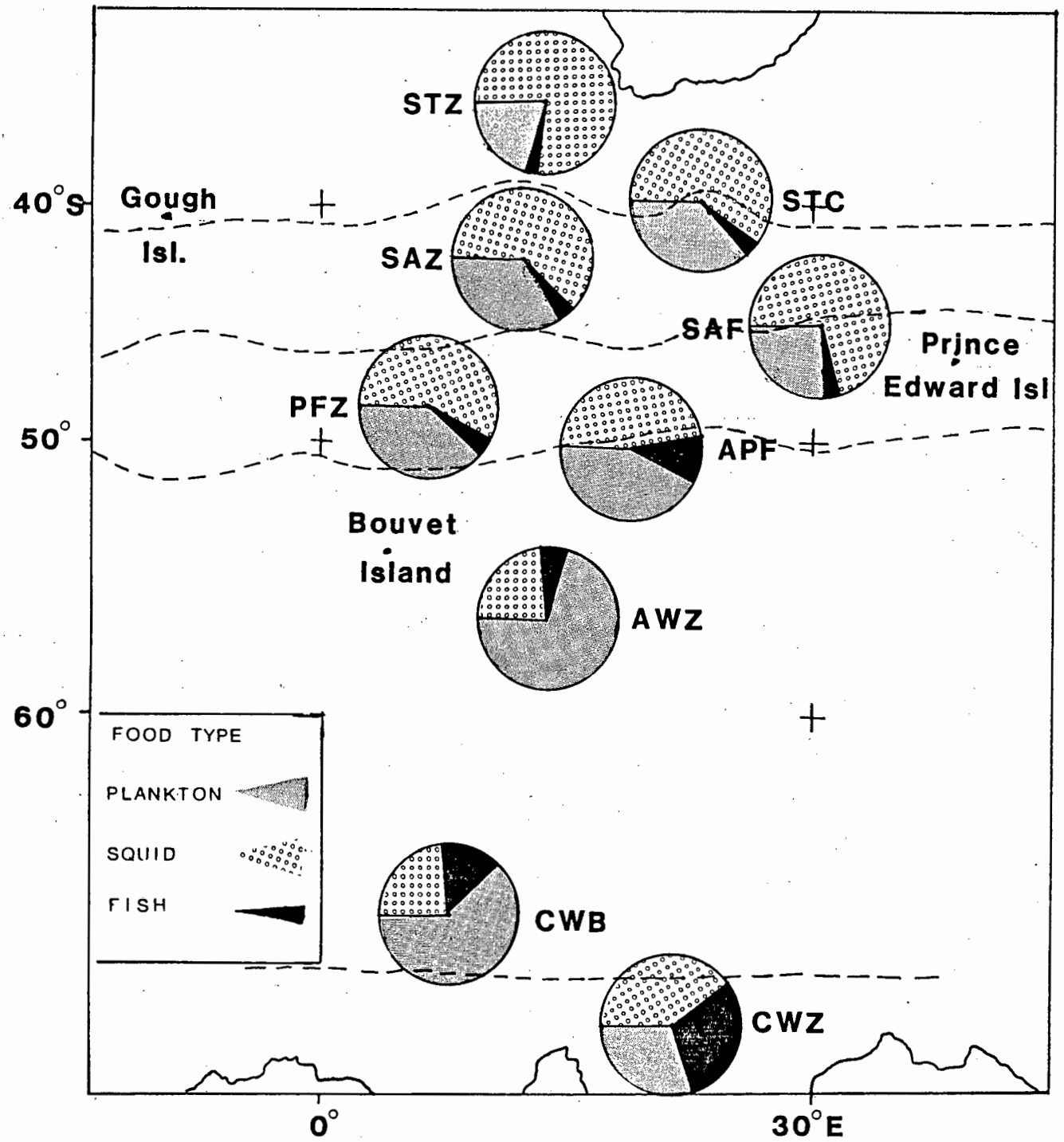
Table 2. Annual prey biomass (g (fr. wt.) m^2) and carbon flux (g C m^2) required by seabirds in the African sector of the Southern Ocean, 1979-81

Zone	Diet class									
	Planktivores		Squid-Eaters		Piscivores		Mixed		Total	
	Biomass	C	Biomass	C	Biomass	C	Biomass	C	Biomass	C
STZ	0.39	0.040	1.57	0.175	0.03	0.003	0.06	0.006	2.05	0.224
STC	0.57	0.061	0.98	0.104	0.02	0.002	0.13	0.014	1.63	0.181
SAZ	0.27	0.029	0.53	0.056	0.01	0.001	0.08	0.009	0.89	0.095
SAF	0.18	0.020	0.51	0.058	0.01	0.001	0.07	0.007	0.77	0.085
PFZ	0.27	0.029	0.43	0.047	0.01	0.001	0.11	0.011	0.82	0.088
APF	0.33	0.035	0.36	0.039	0.04	0.005	0.15	0.016	0.88	0.095
AWZ	0.53	0.058	0.16	0.017	0.02	0.002	0.10	0.010	0.81	0.087
CWB	0.21	0.023	0.07	0.007	0.03	0.003	0.07	0.007	0.38	0.040
CWZ	0.01	0.001	0.03	0.003	0.01	0.001	0.16	0.017	0.21	0.020

Table 3. Daily Flight Energy (DFE, Pennycuick, 1982) as a percentage of Daily Energy Expenditure (Walsberg, 1980) for selected species of seabirds

Species	DEE ($kJ\ d^{-1}$)	DFE ($kJ\ d^{-1}$)	$\frac{DFE}{DEE} \times 100$
Diomedea exulans	5 538	569	10.3
D. melanophris	3 052	354	11.6
D. chrysostoma	3 109	346	11.1
Phoebetria fusca	2 441	300	12.3
Procellaria aequinoctialis	1 509	179	11.9
Daption capense	783	665	84.9
Pachyptila spp.	378	240	63.5
Oceanites oceanicus	157	45	28.8
Macronectes spp.	3 710	440	11.9

Fig. 3. Proportionate distribution of the amounts of seabird food-types based on diets and carbon requirements (g C m^2yr^{-1}) of seabird populations in different zones of the African sector of the Southern Ocean, 1979-1981. See text for explanation of abbreviations of names of oceanic fronts and zones



Discussion

Regional Carbon Flux to Seabirds in the African Sector

In the African sector of the Southern Ocean, the distribution of the different diet classes of seabirds apparently reflects the gross structure of the habitat and availability of prey at the sea surface. Primary production at the Sub-tropical Convergence is higher than at the Antarctic Polar Front (El-Sayed, 1970; Deacon, 1982). Allanson et al. (1982) found relatively high chlorophyll levels during 2 crossings of the Sub-tropical Convergence (40° S). Aerial seabirds required 0.2% of the primary production (93 g C m^2 yr^{-1}) reported for this frontal zone by Holm-Hansen et al. (1977). Seabird density was relatively low in the zones associated with the Sub-Antarctic and Antarctic Polar fronts, where Allanson et al. (1982) found high chlorophyll levels during 1 of 2 crossings. Aerial seabirds required 1.2% of the primary production (8 g C m^2 yr^{-1}) reported for the APF by Holm-Hansen et al. (1977). The seabirds in the Antarctic Water Zone required 0.6% of the C flux, based on productivity (16 g C $m^2 yr^{-1}$) for these latitudes given by Holm-Hansen et al. (1977) and El-Sayed (1978). Seabird energy requirements were lower at the Sub-Antarctic and Polar fronts than in the Sub-tropical Convergence and the Antarctic Water zones (Table 2). Yet, the percentage of C flux to the birds was higher at the Antarctic Polar Front than in the Sub-tropical Convergence or Antarctic Water zones.

The African Sector in a Global Context

The biomass of seabirds (excluding penguins) in the Southern Ocean has been estimated at 48,000 t (Iverson, 1977) and 56,500 t (Prevost, 1981). Based on counts of seabirds at sea, the African

sector of the Southern Ocean contains 31 t yr^{-1} of aerial seabirds, or 0.07% and 0.06% of Iverson's and Prevost's estimates, respectively. Iverson (1977) estimated total annual food requirements for aerial seabirds in the Southern Ocean to be 6.0-8.5 X 10^6t yr^{-1} of krill, squid and fish. Prevost's (1981) estimate was slightly lower (5.5 X 10^6t). The minimum amount of food required by the seabird population in the African sector, based on the data presented here, is 1.4 X 10^4 t , or about 2.0-3.0% of Iverson's and Prevost's totals for the entire Southern Ocean population of aerial species. The area covered by my study is 0.04% of Iverson's area; meaning that my estimates of food consumption are comparable with his.

The sub-tropical region of southwestern Africa (Benguela upwelling system) supported the greatest avian density, requiring between 1.8 and 2.1 g food m^2yr^{-1}. Estimates of food required by breeding birds in the sub-tropical Peruvian upwelling area (11-45 g food m^2 yr^{-1}, Schaeffer, 1970) constitute the only example of a higher seabird food requirement. The deep-ocean avifauna of the eastern Pacific Sub-Arctic zone require less food (0.05-0.10 g food m^2yr^{-1}, Sanger, 1972) than the birds of the sub-Antarctic zones of the Southern Ocean (0.77 - 0.89 g food m^2yr^{-1}). A higher northern sub-polar seabird food requirement (1.9 g food m^2 yr^{-1} by seabirds in the vicinity of an Atlantic Sub-Arctic breeding colony) was reported by Furness (1978).

In polar latitudes (50-65^{o}S) C flux to seabirds in the Southern Ocean (0.087 g C $m^2$0.5 yr^{-1}) was slightly higher than in the polar Bering Sea (0.050 g C $m^2$0.5 yr^{-1}, Schneider and Hunt, 1982). Using a formula more like that of Walsberg (1980) on the same data set, Schneider and Hunt (1982) re-calculated DEE (after King,

1974) which gave a C flux of 0.075 g C $m^2$0.5 yr^{-1} to seabirds in the Bering Sea. This is very close to the values for the Southern Ocean. Whereas Southern Ocean aerial seabirds required 0.1-1.2% of the estimated primary production, the Bering Sea population required 0.02-0.03%, based on primary production estimates by McRoy and Goering (1976). With the inclusion of penguins at the same trophic level as aerial birds (Prevost, 1981), close to 10% of the primary production may be required by the Southern Ocean seabirds.

A composite of Antarctic food-chain models by Nemoto and Harrison (1981) suggests only 2 or 3 trophic levels below seabirds. Sanger (1972) postulates 5 trophic levels below seabirds in the North Pacific. The food chain to Antarctic baleen whales is shorter than that to baleen whales in the North Pacific (Nemoto and Harrison, 1981). The apparently shorter food chain to seabirds in the Antarctic is probably linked with the birds' requirements for a greater proportion of the primary production than in the North Pacific.

Caution is necessary in making generalizations about oceanic primary production and food chains, because the widest variation in productivity values and the greatest degree of plankton patchiness occur in the richest areas (Ryther *et al.*, 1973; Longhurst, 1981). In the past, oceanographic stations were operated on broad spatio-temporal scales (e.g. at 4-6 h intervals). Recently, oceanographers have shown the existence and complexity of small-scale events, *i.e.* 50-150 km diameter (Longhurst, 1981; Lutjeharms, 1981; Owen, 1981; Peterson *et al.*, 1982; Hofmann *et al.*, in press) which probably affect plankton productivity significantly.

Patchy concentrations of nutrients and krill are associated with the Antarctic Water Zone (Makarov et al., 1970; Tranter, 1982). Prey patches at the sea surface must be frequent enough in the zone to support dense patches of plankton-eating birds, since they require frequent meals. Moreover, seabird mobility provides a "constancy in their habitat preferences" on an oceanic scale (Brown, 1980), so that the birds adapt rapidly to different prey distributions. Plankton-eating birds occur more uniformly in high densities over areas where primary production is more uniformly distributed (i.e. the sub-tropical zones) than in high latitudes (i.e. Antarctic Water Zone) where they occur in dense patches in response to patchy prey distribution. Data on prey abundance and distribution, and seabird associations with small-scale oceanographic events, are needed to investigate further the extent to which seabird distribution is influenced by small-scale oceanic events which cause plankton patchiness.

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Appendix 1. Principal food-type classes, body mass (live weight) and percentage abundance (numbers of individuals) of species observed in the African sector of the Southern Ocean, 1979-1981. Percentage abundance is presented for each species in each of the habitat zones as described in text. Food-type classes based on Ashmole (1971) and unpublished records taken from the FitzPatrick Institute which also maintains records of bird weights.

		Mass (kg)	STZ	STC	SAZ	SAF	PFZ	APF	AWZ	CWB	CWZ
Plankton											
Pachyptila spp.	prions	0.15	40.84	57.52	48.07	29.48	48.66	41.01	50.83	27.20	1.06
Haloboena caerulea	Blue Petrel	0.21	0	0.08	3.63	13.65	1.68	1.57	20.09	30.33	1.87
Oceanites oceanicus	Wilson's Stormpetrel	0.04	0.36	0.25	0.44	0.21	0.17	0.17	0.24	0.43	0.86
Oceanodroma leucorhoa	Leach's Stormpetrel	0.05	0.10	0.02	0.03	0	0	0	0	0.24	0
Fregatta tropica	Blackbellied Stormpetrel	0.06	0.13	0.13	0.73	0.59	0.33	1.97	0.83	<0.01	0
Fregatta grallaria	Whitebellied Stormpetrel	0.05	0.03	0.15	0.14	0.16	0.06	0.17	0.02	0	0
Pelagadroma marina	Whitefaced Stormpetrel	0.03	0.01	0.03	0	0	0	0	0	0	0
Hydrobates pelagicus	European Stormpetrel	0.04	0.06	0.01	0.01	0	0.25	0.39	0.19	0.17	0
Pelecanoides spp	diving petrels	0.12	0.42	0.80	0.48	0.86	1.51	1.49	0.15	<0.01	0
Phalaropus fulicarus	Grey Phalarope	0.03	0.03	0.09	0	0.54	1.65	0	0	0	0
Garrodia nereis	Greyrumped Stormpetrel	0.05	0	0.09	0	0.02	0	0	0	0	0
			41.56	59.17	53.53	45.51	54.31	46.77	71.53	57.95	3.79
Squid											
Diomedea exulans	Wandering Albatross	8.60	0.93	1.46	1.03	1.33	0.58	0.48	0.20	0.27	0.11
Diomedia melanophris	Blackbrowed Albatross	3.50	1.52	1.22	2.50	2.37	3.00	0.39	0.18	0.01	0
Diomedia chrysostoma	Greyheaded Albatross	3.60	0.03	0.15	0.90	2.50	1.21	0.13	0.18	0.01	0
Diomedea chlororhynchos	Yellownosed Albatross	2.00	1.04	0.44	0.16	0.06	0.03	0	0	0	0
Diomedea cauta	Shy Albatross	4.10	0.36	0.15	0.52	0.21	0.05	0	0.02	0	0
Phoebetria fusca	Sooty Albatross	2.50	0.31	1.57	0.59	1.05	0.41	0.12	0.18	0.06	0

Phoebetria palpebrata	Lightmantled Sooty Albatross	2.70	0	0.05	0.59	1.45	0.61	0.05	0.22	0.86	0.52
Fulmarus glacialoides	Antarctic Fulmar	1.00	<0.01	0.02	0	0.66	2.64	0.17	1.42	0.37	0.58
Daption capensis	Pintado Petrel	0.45	0.87	1.01	0.65	1.15	1.24	0	0.62	0.39	0.40
Pterodroma macroptera	Greatwinged Petrel	0.58	1.65	1.65	4.09	3.57	1.45	2.80	0.43	0	0
Pterodroma lessonii	Whiteheaded Petrel	0.75	0.21	0.43	3.08	5.65	0.86	1.05	1.26	0.64	0
Pterodroma incerta	Atlantic Petrel	0.52	0.44	1.58	0.63	0.84	0.30	0	0.04	0	0
Procellaria aequinoctialis	Whitechinned Petrel	1.21	2.00	1.50	3.89	3.97	1.38	3.98	0.42	1.27	0.58
Procellaria cinerea	Grey Petrel	1.03	0.04	0.23	0.73	1.41	0.14	0.09	0.01	0	0
Puffinus gravis	Great Shearwater	0.95	34.06	7.61	0.87	0.63	0.80	2.32	0.06	0	0
			43.47	19.07	20.23	26.85	14.70	11.58	5.24	3.88	2.19

Fish

Calonectris diomedea	Cory's Shearwater	0.96	1.81	0.03	0	0	0	0	0	0	0
Puffinus griseus	Sooty Shearwater	0.79	1.50	0.63	0.05	0.28	0.39	9.23	4.07	14.37	0.18
Puffinus puffinus	Manx Shearwater	0.48	0.10	0	0.01	0	0	0	0	0	0
Puffinus assimilis	Little Shearwater	0.23	1.97	4.18	3.55	3.09	0.69	0.22	0.01	0	0
Sterna vittata	Antarctic Tern	0.14	0.04	0.02	0	0	0	0	0	0.01	0.20
Sterna paradisaea	Arctic Tern	0.13	0.27	0.04	0.03	0	0.08	0	0.09	0.52	23.70
Sterna hirundu	Common Tern	0.12	0.37	0.01	0	0	0	0	0	0	0.75
Morus capensis	Cape Gannet	2.90	0.06	0	0	0	0	0	0	0	0
			6.12	4.91	3.64	3.37	1.16	9.45	4.17	14.90	24.83

mixed

Macronectes giganteus	Southern Giant Petrel	4.10	0.05	0.26	0.27	0.70	0.44	0.08	0.27	0.20	0.42
Macronectes halli	Northern Giant Petrel	5.20	0.16	0.20	0.05	0.02	0	0	0	0.10	0.03
Thalassoica antarctica	Antarctic Petrel	0.70	0	0	0	0	0.03	0.52	1.83	12.29	48.37
Pagodroma nivea	Snow Petrel	0.30	0	0	0	0	0	0.09	0.65	2.29	14.96
Pterodroma brevirostris	Kerguelen Petrel	0.33	0.42	4.06	3.26	11.17	12.42	11.94	11.93	8.05	4.71
Pterodroma mollis	Softplumaged Petrel	0.31	7.08	11.86	17.81	10.90	16.52	19.24	3.56	0	0.11
Catharacta antarctica	Subantarctic Skua	1.63	0.09	0.05	0.08	0.08	0	0.13	0	0	0
Catharacta maccormicki	Maccormicks Skua	1.26	0.01	0	0	0	0	0	0.03	0	0
Stercorarius pomarinus	Pomarine Skua	0.67	0.13	0.05	0	0	0	0	0	0	0
Stercorarius parasiticus	Arctic Skua	0.53	0.05	0.12	0.03	0.39	0.03	0.17	0	0	0
Stercorarius longicaudus	Longtailed Skua	0.29	0.07	0	0	0	0	0	0	0	0
			8.06	16.60	21.50	23.26	29.44	32.17	18.27	22.93	68.60

5.1.2. Macro-scale environmental determinants

Environmental determinants of pelagic seabird distribution in the African sector of the Southern Ocean

Abstract. The distribution of birds at sea in the Southern Ocean south of Africa relates to the environmental parameters at regional scale: barometric pressure, salinity, air temperature, water temperature, wind strength and weather. Multivariate regression statistics are used to assess the usefulness of modelling seabird abundance on weather and sea-surface conditions indicated by these variables. The birds' distribution appears most strongly correlated with sea-surface temperature. A variety of possible combinations of cause-effect interactions among the physical parameters (barometric pressure, temperature and wind) revealed low linear correlations between seabird distribution and weather. Linear models explain a consistently small proportion of the spatial variation in seabird distribution and abundance in relation to sea-surface structure. Seabird abundance and sea-surface temperature exhibit strong curvilinear correlations across frontal regions. Thus, the use of abiotic environmental features as predictors of seabird distribution requires non-linear analysis, which suggests that: 1) pelagic seabirds are distributed randomly at sea or, 2) their distribution is non-random as a consequence of a combination of biogeographical history, food requirements, breeding period and locale, and physical environmental features. This hypothesis can only be finally tested with a complex stochastic model, and we lack sufficient data on the distribution of hydrological events which control prey availability to aerial seabirds; this information is necessary for the construction of a model which explains greater than 50% of the variation in the distribution of seabirds. At present, meaningful patterns in the distribution of Southern Ocean seabirds relate to spatio-temporal separation by seabird diet-classes and the distribution of permanent thermal fronts.

Introduction

Seabirds at sea aggregate at certain frontal zones (Griffiths, Siegfried and Abrams, 1982; Schneider and Hunt, 1982; Section 5.1.1) apparently because of food availabe at such sites (Brown, 1980). Hunt et al. (1981) hypothesized that the spatial and seasonal distribution of birds in the Bering Sea was structured in relation to differences in continental shelf water domains. Joiris (1978) demonstrated discrete differences between the avifauna associated with Atlantic and North Sea water masses and hypothesized this to be due to the differences in food availability in the two areas. Pocklington (1979) associated the distribution of certain seabird species with particular water masses which were in turn identified on the basis of temperature and salinity. When Kinder et al. (1983) applied linear regression models to seabird-habitat associations the proportion of variance explained was very low. If regression models can be found which represent seabird-habitat correlations satisfactorily, then seabird dispersion can be used in marine ecosystem analyses as an indicator of the biological structure of the sea-surface.

In a distributional analysis, the birds at sea in the African sector of the Southern Ocean were organized into species-classes which share the same or similar diets, and which probably reflected the availability of different food-types in various oceanic zones (Griffiths et al., 1982). This paper explains pelagic seabird, i.e. all species except penguins, distribution in relation to a generalized surface structure of the African sector of the Southern Ocean. The locations of thermohaline fronts and the habitat zones delineated by them in the Southern Ocean seem stable on a macro-scale (frontal zones of 3-5 degrees of latitude,

Nowlin and Clifford, 1982; Lutjeharms and Valentine, in press). Five hydrological and meteorological variables are used to represent these zones along an environmental gradient from Africa to Antarctica.

Methods

Observations

Seabirds were recorded during fourteen separate cruises of the M.V. S.A. Agulhas April 1979 to May 1982 (Fig. 1). The ship covered nearly the same areas at the same seasons on its regular schedule to research stations (Appendix 1). All birds observed flying past, or passed by, the moving ship (mean speed = 23.4 km h^{-1}) in a 1km-wide transect were counted during 5 878 10-minute (in hour blocks) observation periods (Griffiths, 1981). The ship usually arrived at islands (Prince Edward Islands, Tristan da Cunha group, Gough Island and Bouvet Island) and Antarctica in the early morning, and departed from them in the afternoon. Consequently, observations of seabirds were not made within approximately 100 km of seabird breeding sites.

Analysis

The raw data were mapped by the Southern Ocean Pelagic Seabird plotting program (Abrams et al., 1981), which averages all observations in a given cell area (two degrees in this study) and prints values or symbols on an approximate mercator projection (Figs 2 and 3).

The trophic structure of seabird assemblages was assessed in terms of abundance (total number of all birds at an observation station) and biomass (total live-weight of all birds at an observation

station) of seabirds in four diet-classes (defined as in Appendix 2; abbreviations throughout for diet-classes are: plankton (PF), squid (CF), fish (FF), mixed-diet (MF)). The ecological structure of the avifauna was assessed by identifying associations between seabirds and environmental conditions or features. The relative strengths of these associations were assessed by comparison of the coefficients of correlation (r) or coefficients of determination (R^2) between seabird abundance and air temperature (AIR), sea-surface temperature (WAT or SST), barometric pressure (BAR), wind strength on Beaufort Scale (WIND) and weather (WEATH) coded from 1 (clear sky) to 6 (storm with rain or snow). These weather codes were a reduction in the number of variables contained in the World Meteorological Office codes. They represent a continuum of dry to cloudy to wet weather conditions.

In this study, the set of environmental variables presented were the best and most consistently available from a majority of cruise logs to represent weather patterns and latitudinal changes in the sea surface. Changes in air and sea-surface temperatures reflect changes in marine habitat structure because air temperature at the sea surface is correlated with sea surface temperature due to evaporation and sensible heat transfer (Viebrock, 1962). Seabirds capable of flight are active within 20 m of the sea-surface and probably sense changes in their environment through air-sea interactions (Manikowski, 1971; Shuntov, 1974; Kinder et al., 1983). The sea-surface temperatures and positions associated with fronts and zones in the African sector of the Southern Ocean (Fig. 1) are described by Deacon (1982), Clifford (1983) and Lutjeharms and Valentine (in press).

Principal Components Analysis with orthoganal rotation was used to

identify covariates on a broad oceanic scale (BMDP4M, Dixon, 1981, with total abundance and biomass excluded due to multicolinearity). Finer scale analysis of biotic-abiotic relationships was performed using 'Best subset regression analysis' (BMDP9R), which tests all possible biotic-abiotic correlations using stepwise multiple regression, and provides coefficients of determination as a measure of the biotic - abiotic parameter covariation. This program tests each selected biotic variable against each abiotic variable alone and in combinations of 2,3.....n independent variables (five in this study).

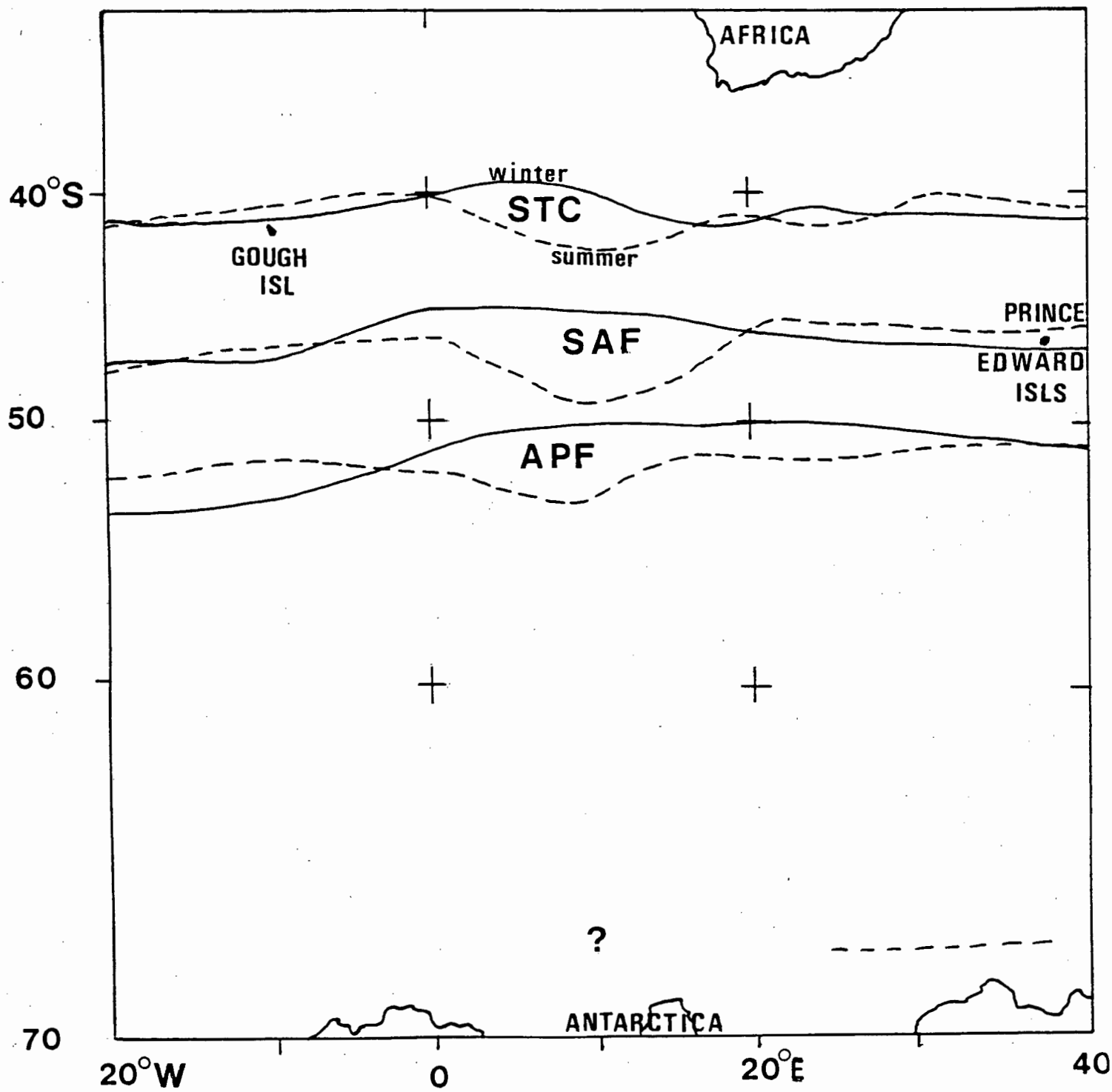
Data analysed in annual or regional composites were also analysed as segments of cruise tracks. Continuous bird and temperature data across frontal zones were plotted and further analysed. In some cases a linear fit of the bird abundance to SST was obtained by (log + 1) transformation of the bird data. Where a log-linear model was inappropriate, a Gaussian shaped curve was fit to the change in bird abundance with respect to SST. The Gaussian equation was used to model seabird abundance on SST:

$$f(x) = P1e^{\frac{-(X-P2)^2}{2P3}} \qquad (1)$$

where P1 is a scalar value for the bird abundance (y-axis), P2 is the SST associated with the peak in bird abundance and P3 is a scalar parameter which represents the breadth of the peak of seabird abundance in terms of SST (x-axis). The curve was fitted for each cruise track separately using the maximum likelihood

estimator of the least squares regression provided by BMDPAR 1982 (Dixon, 1981). This program fits a curve to a bivariate data set according to a standard convergence criterion. The bird abundance data for each cruise track were then transformed using the curve parameter values (P1, P2, P3) determined by the curve fitting program to characterize the relationship between seabird abundance and SST on that cruise. The linear regression of the predicted (transformed) versus observed bird abundances was a measure of the relative strength of a relationship which states that seabirds were significantly clumped at the thermal signature of the front. An attempt was then made to find an equation which might serve as a general predictive model for seabird abundance at oceanic fronts or convergences. This required establishing bird abundance criteria for species or groups of species which indicate the presence of an oceanic feature of biological importance.

Fig. 1. African sector of the Southern Ocean showing area covered in 14 voyages of the M.V. S.A. Agulhas, 1979-1982 (Appendix 1). The winter (solid lines) and summer (dashed lines) mean positions of the Sub-tropical Convergence (STC), and Sub-Antarctic Front (SAF) and Antarctic Polar Front (APF) are presented.



Results

The habitat

On the basis of air and sea-surface temperature, and climate, the African sector of the Southern Ocean contains at least three discrete zones: the sub-tropical, sub-Antarctic and Antarctic (Table 1; Fig. 1; Baker, 1979; Deacon, 1982). The sub-tropical zone includes the Agulhas and Benguela Currents, and a complex retroflection and mixing zone between these and the Antarctic Circumpolar Current, presently referred to as the Sub-tropical Convergence zone (STC, Lutjeharms, 1981). The sub-Antarctic zone is dominated by the Antarctic Circumpolar Current, which is among the world's strongest and deepest flowing currents (Munk, 1955). This zone contains the Sub-Antarctic and Antarctic Polar thermohaline fronts (SAF and APF, respectively, Tranter, 1982; Lutjeharms and Valentine, in press). The Antarctic water zone (AWZ) includes the interface of the Antarctic Circumpolar and East Wind Drift currents and the sea-ice areas and the Antarctic Continental Shelf. Between the Antarctic Polar Front and the Continental water boundary (CWB), a well mixed stable surface layer exists with high mass transport along the front (Nowlin and Clifford, 1982; Tranter, 1982). Southern Ocean fronts and mixing zones are particularly rich in nutrients and plankton (Foxton, 1956; El-Sayed, 1970; Emery, Milliman and Uchupi, 1973; Holm-Hansen *et al.*,1977; Deacon, 1982).

Seabirds and the habitat at macro-scale

Macro-scale habitat-types (*i.e.* the biogeographical zones; sub-tropical, sub-Antarctic, Antarctic) have associated with them particular seabird assemblages (*i.e.* latitudinal zonation of the

Table 1. Mean values of air temperature, sea surface temperature, barometric pressure, wind strength (Beaufort scale) and weather code (1 clear, dry to 6 stormy, wet) for the sub-tropical, sub-Antarctic and Antarctic pelagic regions of the African sector of the Southern Ocean, for 1979-80 and 1980-81. Range of all values in brackets.

	sub-tropical		sub-Antarctic		Antarctic	
	1979-80	1980-81	1979-80	1980-81	1979-80	1980-81
AIR T	13.7+3.0	14.3+4.1	5.3+3.3	5.5+2.8	-0.5+2.3	0.2+1.5
(^{o}C)	(1.0-23.0)		(0-17.0)		(-10.0-10.0)	
SEA T	14.0+3.5	16.6-4.5	4.2+3.0	5.6+2.9	0.6+0.6	1.2+1.2
(^{o}C)	(10.0-26.0)		(-0.3-17.0)		(-1.3-3.0)	
BAR	1016+10.3	1016+7.9	1000+13.1	1004+11.4	983+11.0	991+8.0
	(987-1039)		(960-1027)		(960-1010)	
WIND	5.3+1.5	5.4+1.5	6.0+1.6	6.2+1.5	4.8+1.6	4.8+1.9
	(1.0-9.0)		(1.0+10.0)		(0-10.0)	
WEATH	2.4+0.9	2.5+1.2	2.9+1.1	2.9+0.9	2.8+1.2	3.1+1.2
	(1-6)		(1-6)		(1-6)	

Table 2. Means (standard deviations) per 10 minute observation of abundance (numbers of individuals), biomass (live weight) and abundance of four food-type classes by latitudinal region and year in the African sector of the Southern Ocean, 1979-1988.

	sub-tropical		sub-Antarctic		Antarctic	
	1979-80	1980-82	1979-80	1980-82	1979-80	1980-82
N obs.	1174	1331	846	943	985	1086
Abundance	26.8(169.8)	20.7(88.8)	23.2(42.2)	9.2(19.5)	25.1(124.0)	15.9(72.
Biomass(kg)	18.8(160.4)	10.0(47.9)	9.9(12.1)	5.0(10.4)	9.3 (33.8)	5.3(19.
Plankton	10.6 (38.3)	12.3(78.3)	13.1(41.1)	4.6(16.8)	15.4(119.7)	9.1(60.
Cephalopod	12.3(165.3)	4.2(34.9)	2.8 (3.6)	1.5 (2.3)	0.7 (1.8)	0.6 (3.
Fish	0.9 (1.9)	1.6(11.1)	0.7 (5.3)	1.2 (9.0)	0.9 (7.4)	4.4(38.
Mixed	2.9 (4.4)	2.7(10.5)	6.5 (8.6)	2.0 (2.9)	8.2 (34.0)	1.7 (5.

avifauna, Table 2). Latitudinal zonation of the aerial avifauna in the Southern Ocean has been described by Shuntov et al. (1981a) for areas between 80°E through 180° to 80° W longitude. My results extend the record of latitudinal zonation of seabirds to include 55% of the Southern Ocean. Shuntov et al.'s (1981b) data, which span 13 years, include annual variations in pelagic counts of up to 100%, as do my data for two years (1979-80 and 1980-81, Table 2). It is unlikely that the absolute size of the populations of Southern Ocean seabirds changed by 50%, as appears to be the case between two years in the sub-Antarctic zone (Table 2), since Croxall (1984) reports low adult mortality at sea.

The sub-tropical avifauna was concentrated along the sub-Tropical frontal zone, where squid-eating Procellariiformes dominated the avifauna (in biomass), although large aggregations of planktivores occurred (Fig. 3, Table 2). The Antarctic avifauna was very patchy (Figs 2 and 3); large aggregations of planktivores dominated in abundance (Fig. 2, Table 2). At sea, avian diet-classes were independent of each other (Table 3) presumably due to differences in the distribution and availability of their prey. The predominance of squid-eating birds to the north and planktivores to the south (Figs 2 and 3) coincided with the warm to cold (Africa-Antarctica) environmental gradient. This relationship was not reflected by a Principal Components Analysis which showed relative independence of seabird variables from environmental variables over two successive years (Table 4).

Fig. 2. Pelagic distribution of planktivorous seabirds in the African sector of the Southern Ocean, 1979-1981 (after Fig. 1, Section 5.1.1).

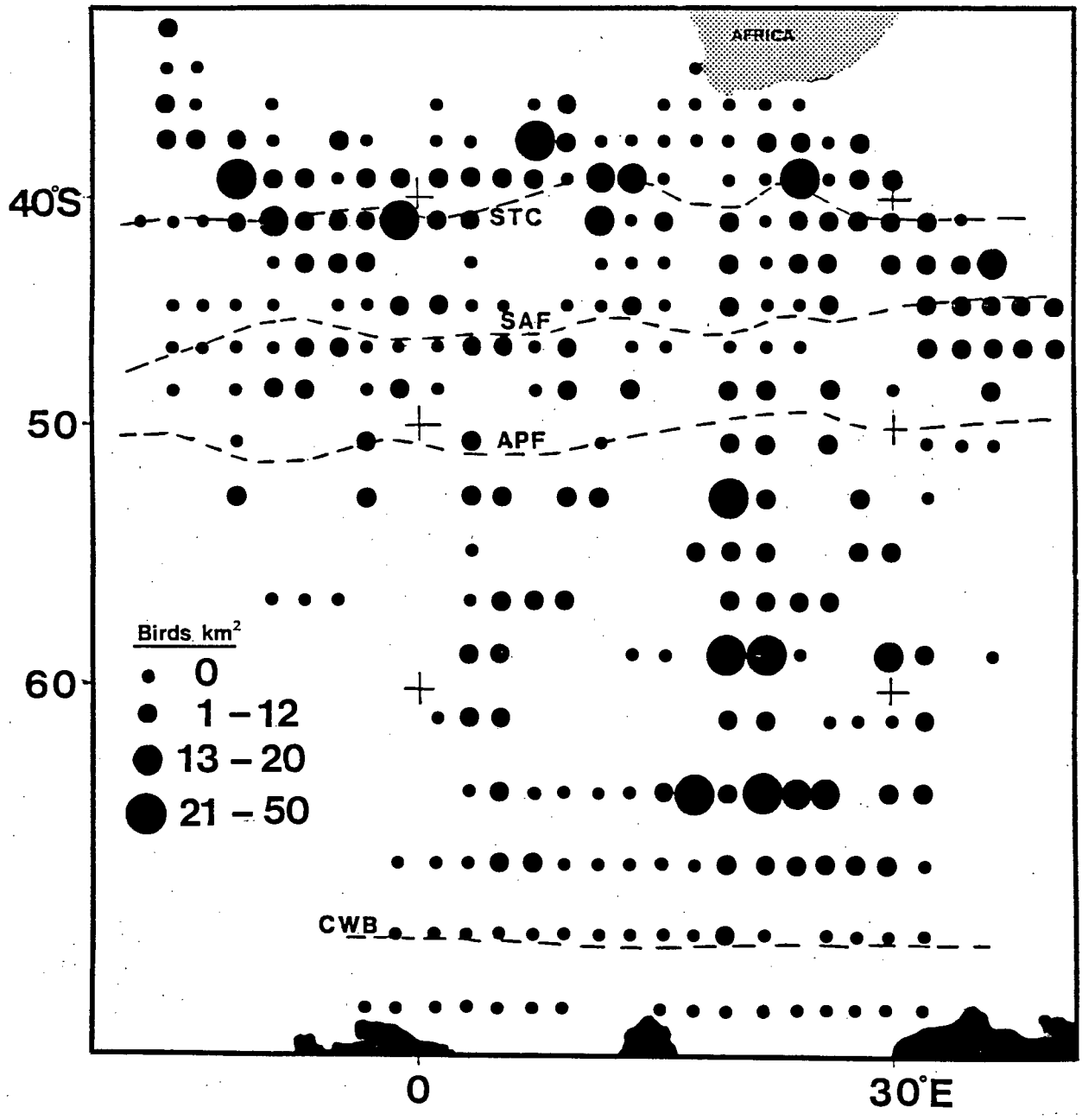


Fig. 3. Pelagic distribution of cephalopod-eating seabirds in the African sector of the Southern Ocean, 1979-1981 (after Fig. 2, Section 5.1.1).

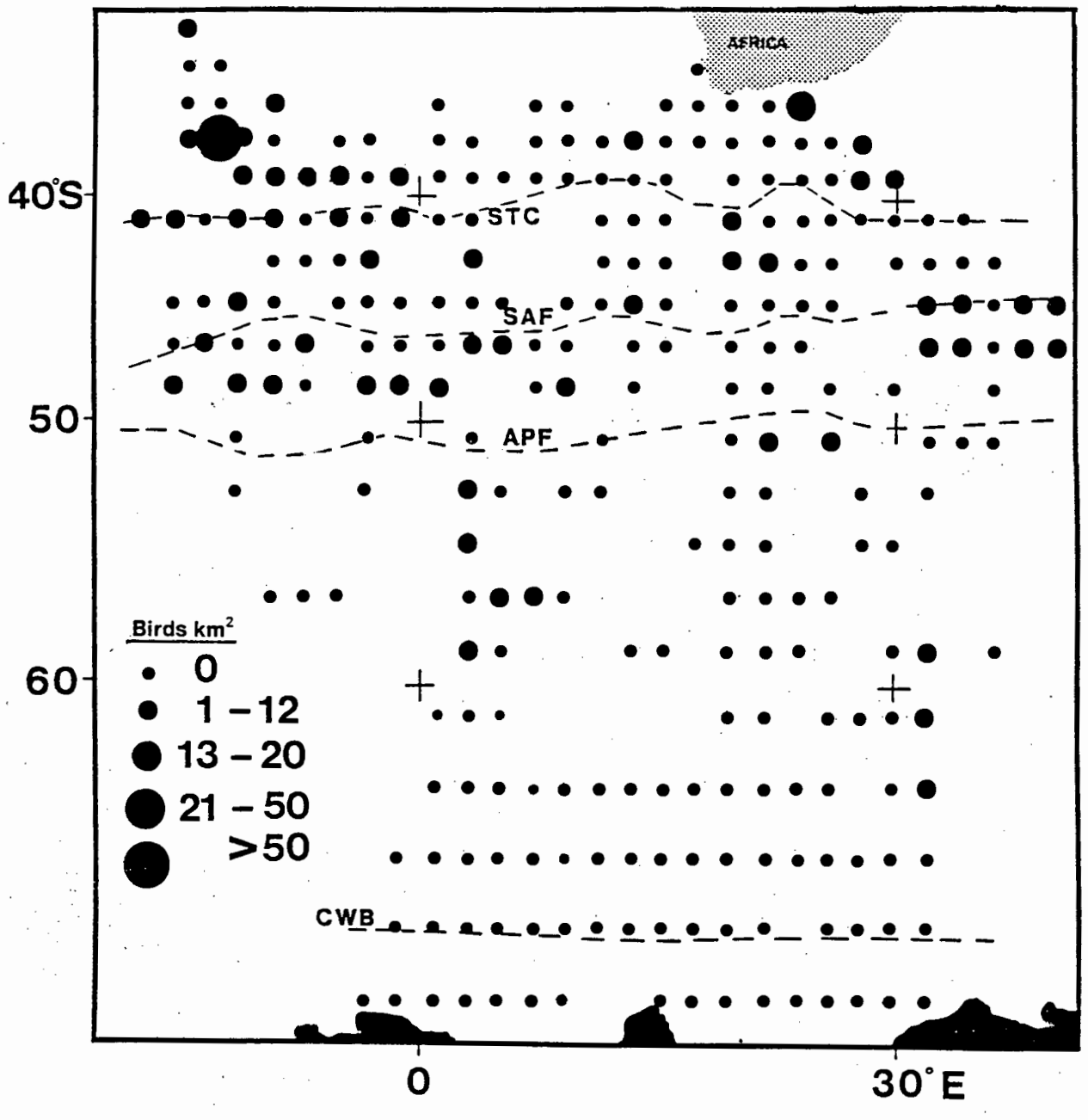


Table 3. Coefficients of correlation (r) between numbers of individual seabirds ordered by four principal diet-classes in three latitudinal regions of the African sector of the Southern Ocean during 1979-80 (A) and 1980-81 (B).

		Plankton	Cephalopods	Fish
sub-tropical				
Cephalopods	A	0.101	1.000	
	B	0.306	1.000	
Fish	A	0.113	0.278	1.000
	B	0.191	0.272	1.000
Mixed	A	0.009	0.144	0.104
	B	0.226	0.318	0.234
sub-Antarctic				
Cephalopods	A	-0.014	1.000	
	B	0.161	1.000	
Fish	A	0.042	0.131	1.000
	B	-0.051	0.052	1.000
Mixed	A	-0.004	0.166	0.147
	B	-0.045	0.261	0.155

Table 4. Principal Components Analysis showing covariations among bird species richness (BSR), species diversity (BSD), numbers of individuals in four diet groups, air temperature, sea surface temperature, barometric pressure, wind strength and weather during 1979-80 and 1980-81 in the African sector of the Southern Ocean. Rotated (orthogonal method) factor loadings indicate relative strength and direction of each contributing variable for factors with Eigenvalues greater than 0.9 (variables with factor loadings between -0.275 and 0.275 are disregarded). Percentage of total variance explained by each factor is presented.

1979-80

PC1		PC2		PC3		PC4		PC5		PC6	
AIR	0.957	BSR	0.940	PF	0.895	WIND	0.983	FF	0.866	WEATH	0.959
WAT	0.942	BSD	0.872	MF	-0.424			MF	-0.432		
BAR	0.856	CF	0.689								
CF	0.345	MF	0.556								
MF	-0.345	FF	0.311								
%var	29.3		22.2		10.6		9.5		7.8		7.2

1980-81

WAT 0.964	CF 0.873	FF 0.806	MF 0.950	PF 0.968	WEATH 0.948
AIR 0.960	BSD 0.872	WIND -0.752	BSR 0.279	BSR 0.321	
BAR 0.842	BSR 0.869				
	FF 0.286				
	WIND 0.286				
%var 29.0	24.3	11.8	8.2	7.6	6.1

Table 5. Coefficents of determination (R^2) and sign of relationship between seabirds grouped by principle diet and habitat variables. Strongest associations for 1979-1981 are presented ($P<0.01$) for zonal scale analyses. Sample sizes as in Table 3.

Diet	Zone	Variables	R^2
Plankton	sub-tropical	-AIR, -WAT	0.26
	sub-Antarctic	-AIR, -WAT	0.18
		-BAR, -WIND, -WEATH	0.13
	Antarctic	-AIR, WAT, WIND	0.17
		AIR, WAT, -BAR	0.17
Cephalopods	sub-tropical	-AIR, -WAT	0.06
	Antarctic	AIR, BAR, WIND	0.09
Fish	sub-tropical	-WAT, -WIND	0.07
	sub-Antarctic	WAT, -BAR, WEATH	0.05
	Antarctic	-AIR, -WIND, BAR	0.31
		-AIR, -WAT, -WIND	0.30
Mixed	sub-tropical	-AIR, -WAT, -BAR	0.18
	sub-Antarctic	-WAT, -BAR, WEATH	0.12
	Antarctic	-WAT, WIND, -BAR	0.04

The avifauna of the oceanic zones differed in terms of the dominant seabird species and diet-classes (Table 2). At zonal scale as much as 30% of seabird distribution can be explained in terms of the environmental gradients characteristic of each zone (Table 5). In the sub-tropical zones, squid-, and plankton-eating bird abundance correlated with cool waters, which represented the STC zone or pockets of water of similar SST (i.e. 11-17^{o}C, Figs 2 to 5). South of the APF, the abundance of planktivores correlated with SST of 1-3^{o}C (Figs 2,4, Table 5), which were relatively warm SST's for the Antarctic region (Table 1). Fish-eating species in the Antarctic zone occurred in calm conditions and cold water, which were typical near Antarctica (Table 5).

Seabirds and the habitat at meso-scale

Seabird-temperature correlations analysed by single cruise tracks were stronger (Tables 6 and 7) than when the cruises were lumped (Table 5). Correlations between the birds and habitat parameters were masked when data from different seasons or ecological zones were lumped. Analyses of subsets of data for which the majority of the birds sighted were behaving in the same way reduced the biological 'noise' in correlation analyses (i.e. the individual birds observed during one cruise would be in the same phase of their annual cycle and such observations would not likely include birds about to return to their breeding site as well as birds just departing from breeding, as would occur in lumped data).

The Cape Town to Prince Edward Islands cruises were in spring (when adults are migrating to breeding sites) and autumn (when breeding birds disperse for winter foraging). In spring as much as 38% of planktivore distribution correlated with cold

Table 6. Coefficients of determination (R^2) and sign of relationship between seabirds grouped by principle diet and habitat variables during Spring (Sept.-Oct.) and Autumn (April-May) for single cruise tracks between Cape Town, South Africa, and the Prince Edward Islands. Strongest associations are presented ($P<0.01$)

Diet	Season	n	Variables	R^2
Plankton	Spring	70	-AIR, WAT	0.38
		73	-AIR, -WAT, -BAR, -WIND, WEATH	0.48
	Autumn	73	-AIR, -WAT, BAR, -WIND	0.43
		64	AIR, WAT, -WIND, WEATH	0.19
Cephalopods	Spring	70	BAR, WEATH	0.19
		73	-AIR, -WAT	0.35
	Autumn	73	AIR, WIND, -WEATH	0.11
		64	AIR, WAT	0.13
Fish	Spring	70	-AIR, -WIND	0.23
		73	AIR, WAT, -BAR, -WEATH	0.31
	Autumn	73	BAR, -WIND	0.29
Mixed	Spring	70	-AIR, BAR, WIND	0.15
		73	-AIR, -WAT	0.11
	Autumn	73	AIR, -BAR	0.24
		64	-AIR, BAR, WIND	0.23

Table 7. Coefficients of determination (R^2) from canonical correlations of seabird abundance by diet-classes with environmental variables (abbreviations as in text). Data are from cruises between Cape Town (C) and Marion Island (M) which is part of the Prince Edward Island group, shown as month/yr/route. Relative contributions of each variable in brackets.

	canonical variable		
Cruise	dependent	independent	R^2
Spring			
9/79/CM	PF(.894)	AIRT(-.629)	0.40
	FF(.964)	WINDS(-.628),BAR(.569)	0.25
	MF(.948)	WINDS(.829),BAR(.652),AIRT(-.574)	0.18
9/80/CM	PF(.855),FF(-.522)..	AIRT(-.793),BAR(-.784),SST(-.601)	0.32
9/80/MC	PF(.819),FF(-.477)..	SST(-2.393),BAR(1.438),WINDS(-.822), WEATH(-.652),AIRT(-.513)	0.54
	CF(.939),MF(.405)...	SST(-.956),AIRT(1.311),WEATH(-.704)	0.39
10/81/CM	CF(.857)	AIRT(1.164)	0.33
	PF(1.022)	AIRT(-4.367),BAR(-2.161),SST(2.437)	0.24
11/81/MC	FF(.539)	AIRT(1.995),BAR(-1.823),SST(.633)	0.62
	PF (.907),FF(.729)..	BAR(-1.986),AIRT(.800),SST(.655)	0.24
Autumn			
4/81/CM	PF(.715),FF(.460)...	SST(2.398),BAR(1.743),AIRT(-1.132), WINDS(-.745)	0.53
	MF(.951)	BAR(-1.165),AIRT(-1.453),SST(.724)	0.26
5/81/MC	MF(.656),PF(-.468), CF(-.431)	AIRT(-2.397),SST(1.094),BAR(-.605,) WINDS(.549)	0.46
6/81/CM	MF(.713),PF(.507)...	BAR(-2.309),AIRT(1.311),WEATH(-.704)	0.48
6/81/MC	FF(.726)	WINDS(-1.447),WEATH(.796),SST(.757), AIRT(-.616)	0.72
	PF(.652),MF(-.541), CF(.508),FF(.492).	SST(-1.344),WEATH(-.933)	0.48
	CF(.730),FF(.515), MF(.494)	AIRT(4.168),BAR(2.362),SST(-2.224)	0.35

Fig. 4. Mean number of individual seabirds in plankton (solid line), cephalopod- (dashed line), fish- (dotted line), and mixed-diet (dot-dashed line) classes associated with sea-surface temperatures for 1980-1981 study season in the African sector of the Southern Ocean. Front labels as in text at approx. SST.

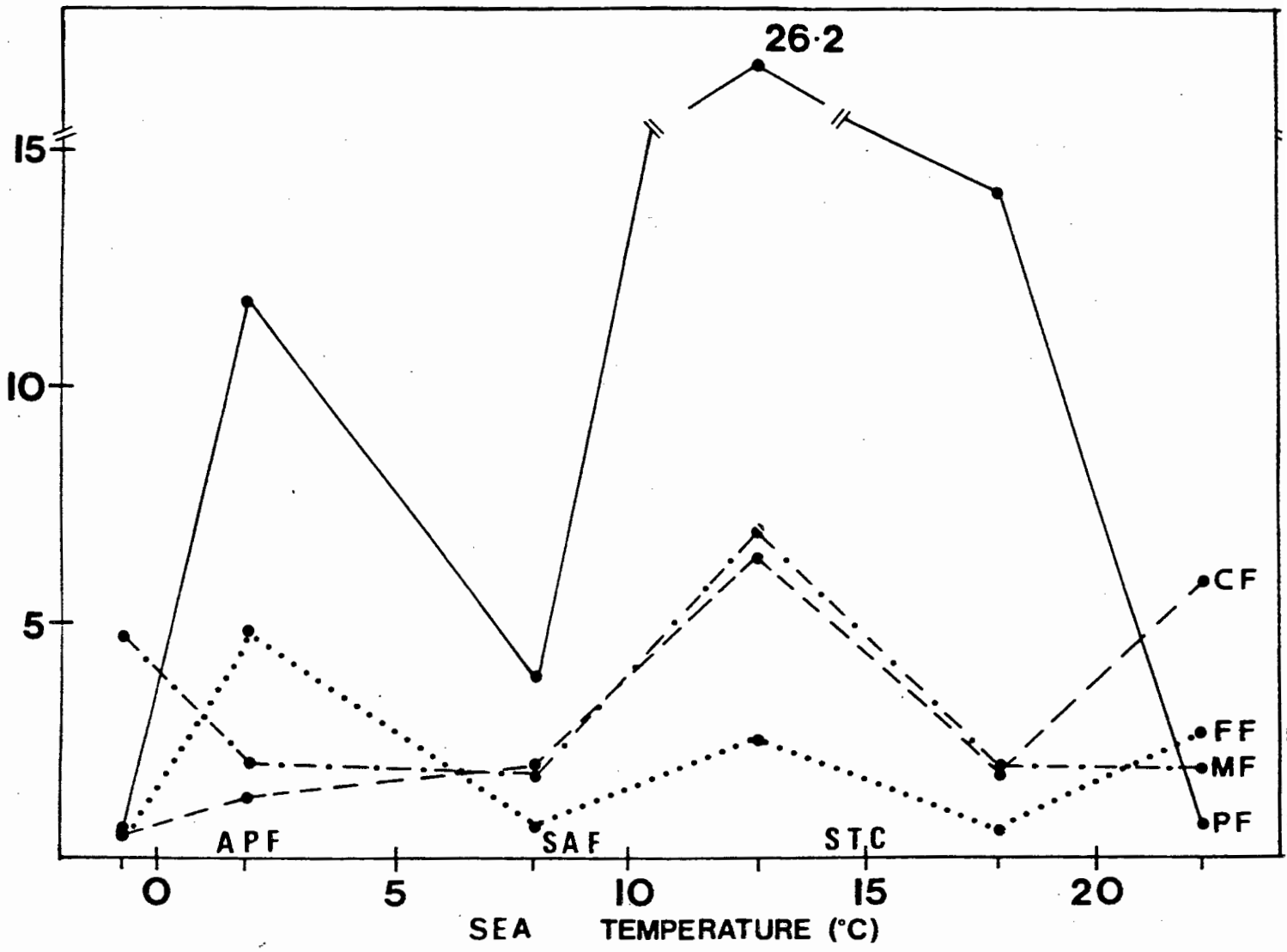
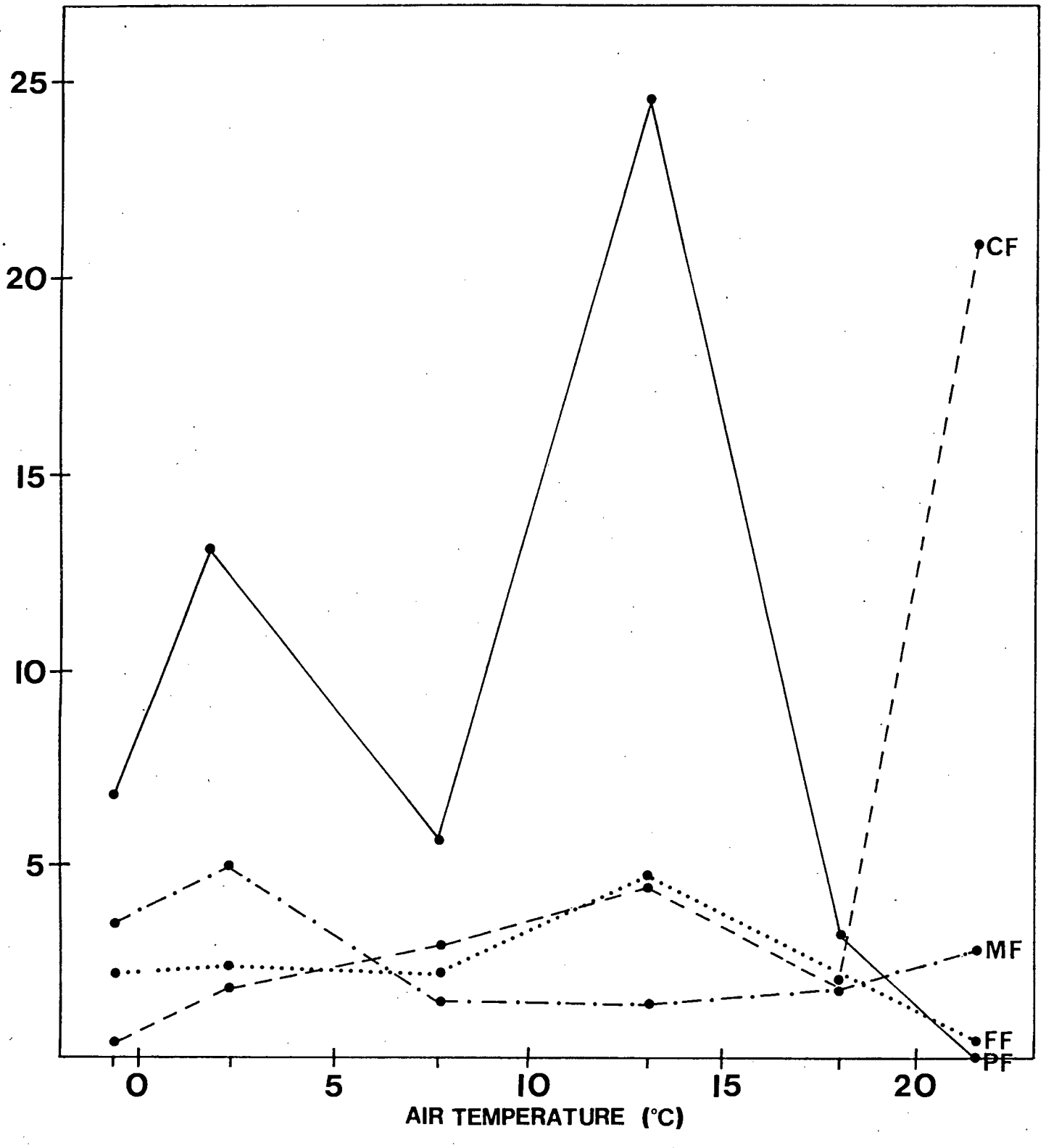


Fig. 5. Mean number of individual seabirds in plankton (solid line), cephalopod- (dashed line), fish- (dotted line), and mixed diet (dot-dash line) classes associated with air temperature for 1980-1981 season in the African sector of the Southern Ocean.



temperatures between Cape Town and the Prince Edward Islands (Table 6). In autumn, the abundances of some species, especially the squid-eaters, correlated with warmer conditions. When seabird diet-classes were combined in canonical correlations with habitat variables, during spring, planktivores associated with cold temperatures and calm weather (Table 7). Squid-eating seabird abundance correlated with warm areas, the abundance of piscivores correlated with warm areas and good weather (Table 7). During autumn, the abundances of planktivores and piscivores correlated with warm, clear conditions (Table 7). At this season, the abundance of most species correlated with good weather and warm air. Most species shifted from warm to cold SST as winter approached (Table 7).

Graphical data (Figs 2-5) and linear-model regression analyses (Tables 4-7) indicated that each cruise track should be broken down into segments which cross areas or SST's associated with fronts. The Sub-tropical Convergence is a zone of oceanic mixing. The fronts move north in winter and south in summer (Clifford, 1983) and the birds of the sub-tropical and sub-Antarctic zones form a mixed assemblage in this broad STC zone. Seabird abundance-maxima occur as a series of Gaussian-distribution curves, which, when lumped, give the impression of one maximum across the STC zone (Figs 4 and 5). Further analyses concentrate on the clumping of seabirds at temperature signatures of the series of thermohaline fronts which occur within the STC zone and between Africa and the Antarctic zone (Lutjeharms and Valentine, in press).

A simple curvilinear model of seabird abundance and SST

During six spring, eight summer and six autumn cruise tracks

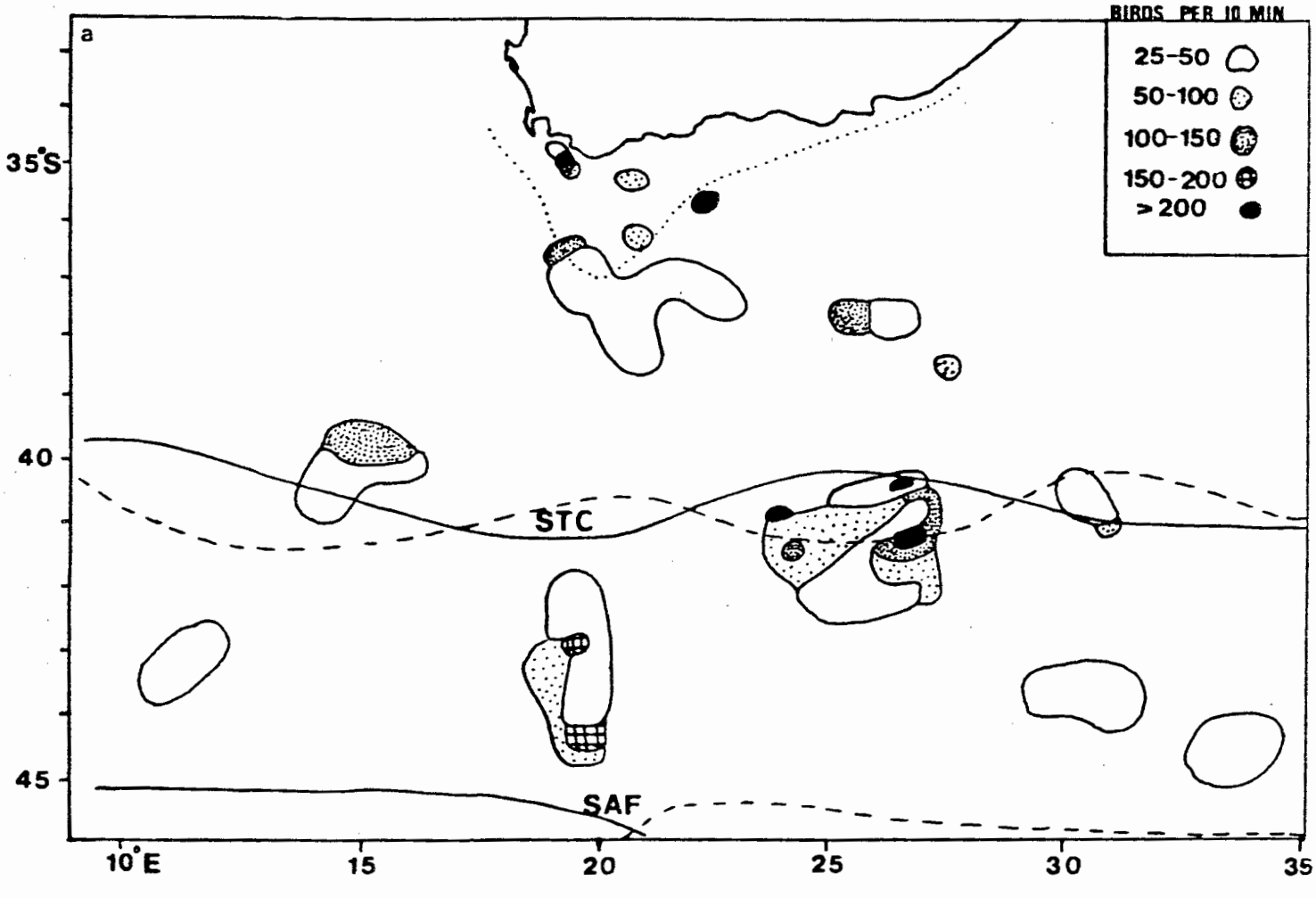
between Cape Town and the sub-Antarctic waters (i.e. en route to Antarctica or the Prince Edward Islands) seabirds were counted continuously as the vessel crossed latitudes associated with the Agulhas Current thermal fronts (AGF, 36 to 37°S), the Sub-tropical Convergence zone (STC, 39 to 41°S) and the Sub-Antarctic Front (SAF, 42 to 45°S). Seabird concentrations occurred in the vicinity of the STC zone, the African continental shelf edge (northern edge of the Agulhas current) and north of the SAF zone (Fig. 6).

During spring (Sep.-Nov.) birds were significantly clumped on 5 of 6 cruises across 35-45°S (Fig. 6, Appendix 3). The SST's with which birds associated became progressively warmer as summer approached (12.4-20.1°C, Appendix 3). On seven of eight summer cruise tracks maximum bird abundance was significantly associated with SST's which were warmer than during spring (13.4-21.1°C), except for the SAF (Fig. 6, Appendix 3). During autumn (April-June) only three of six of the cruise tracks showed significant clumping of birds, and these were at a wide range of SST (8.7-17.9°C, Fig. 6, Appendix 3).

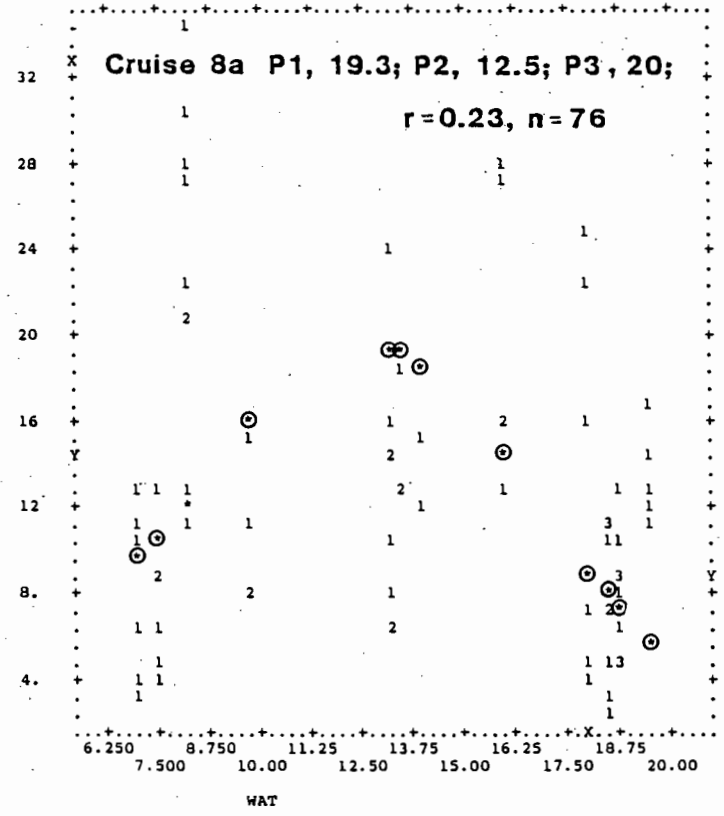
When the association of bird abundance with SST was treated by a curvilinear model, the relative strength of the association exceeded any results obtained using linear models. Spring cruises provided the best fits of the curvilinear model (Fig. 6). In two cases the correlation was high; $r > 0.90$. In summer half the explained variances were greater than $r = 0.40$, while bird abundances were generally lower than during spring. In autumn, the explained variances were not particularly high (Fig. 6).

For the 26 crossings which produced fits to the Gaussian curve, coefficients of correlation, r, increased significantly with

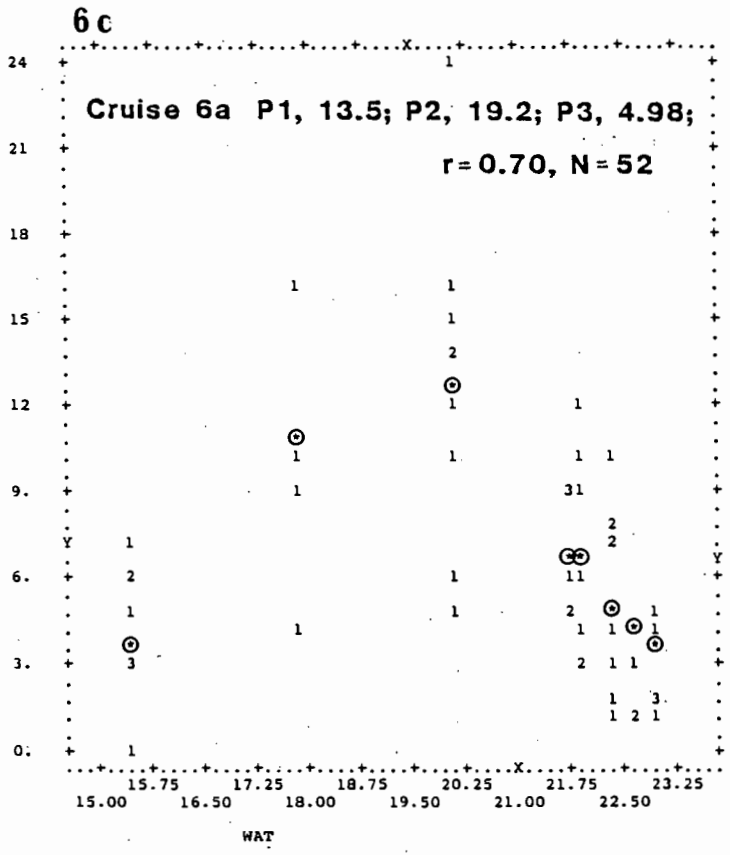
Fig. 6. Seabird distribution where total abundance (TOT) exceeded 25 individuals per observation, (a) in relation to the African continental shelf, Sub-tropical Convergence zone (STC) and Sub-Antarctic front (SAF) (solid line, winter; broken line, summer). Graphs and statistics for three examples of curvilinear model showing typical results for (b) spring, (c) summer and (d) autumn. A measure of the fit (r) between predicted (*) and observed (numerals) seabird abundances in relation to SST^{o}C (WAT) are shown with the Gaussian-curve parameter values (P1, P2, P3).



6d


Cruise 8a P1, 19.3; P2, 12.5; P3, 20;
r=0.23, n=76
WAT

6c


Cruise 6a P1, 13.5; P2, 19.2; P3, 4.98;
r=0.70, N=52
WAT

6b

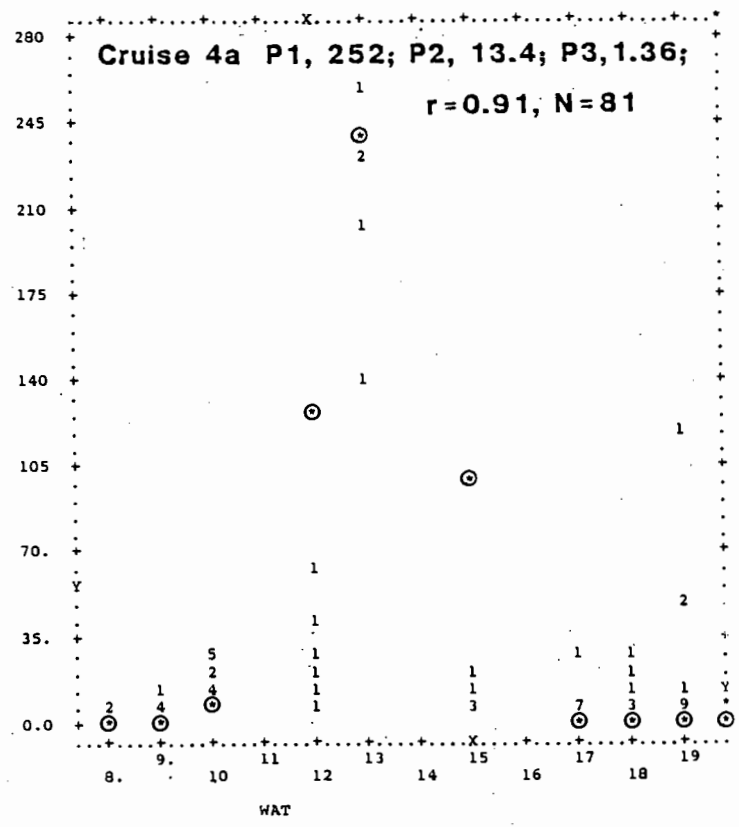
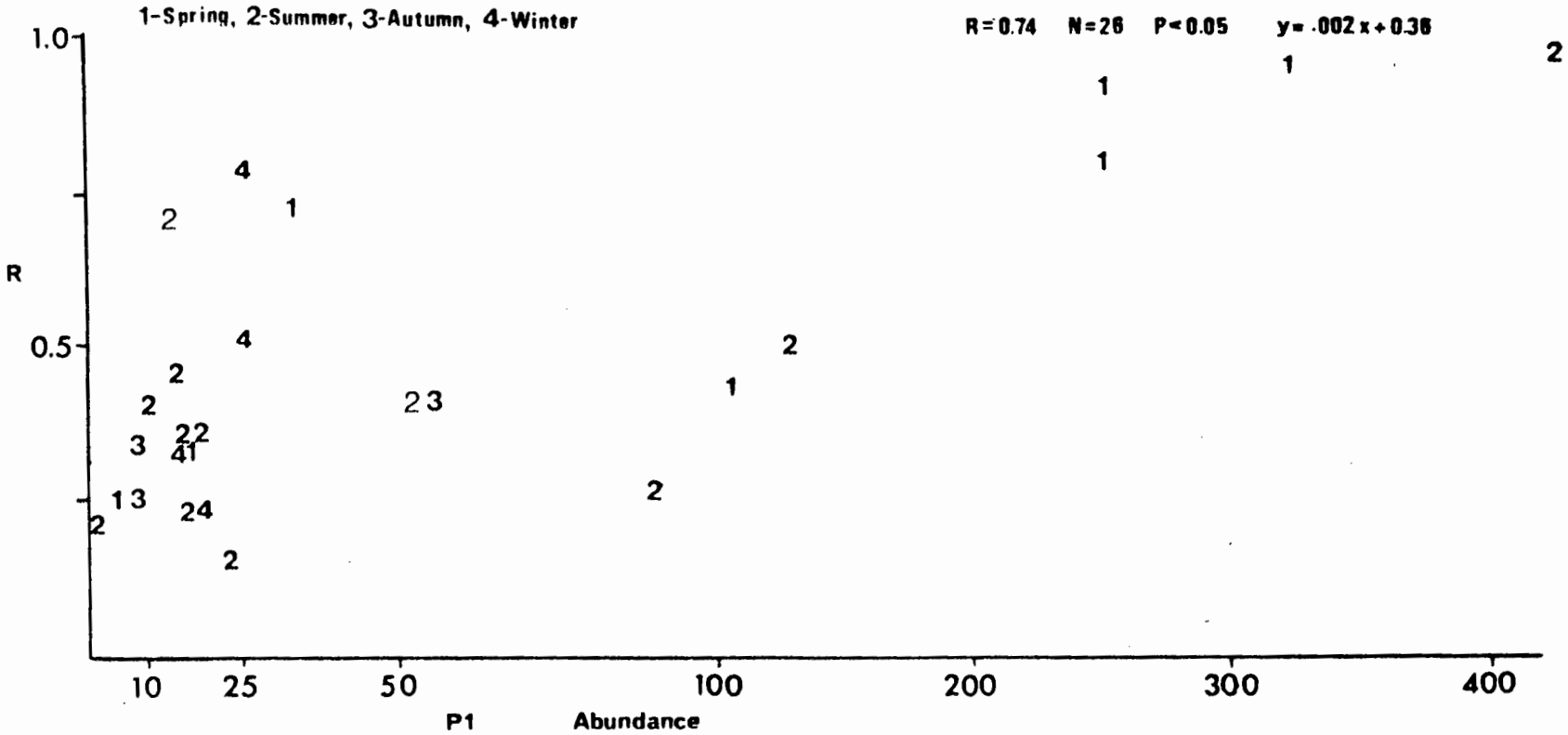

Cruise 4a P1, 252; P2, 13.4; P3, 1.36;
r=0.91, N=81
WAT

Fig. 7. Proportion of variance explained (r) by Gaussian-curve model in relation to maximum total bird abundance (P1 of equation 1) for 26 cruise tracks between Cape Town and Marion Island. Data points represented by season numerals.



increases in the scalar parameter for peak abundance (r vs. P1, r=0.74, P<0.05, Fig. 7). In order to determine if total abundance is the most appropriate index for studying seabird-SST associations, the variance of birds by single species or by plankton-, squid-, fish-, and mixed-diet classes was compared with those for total abundance.

Model driver species

The best fit of the curvilinear model is accounted for primarily by prions in September, 1979 and 1980 at the STC (Fig. 6); Softplumaged Petrels and Blackbrowed Albatrosses were of secondary importance in SST correlations. In November (Fig. 6) terns and Softplumaged Petrels fit the model well at the STC. The strong association of SST with Softplumaged Petrels in November 1981 was not a 'typical' arrangement of single species. In November 1981, the regression of terns alone was slightly higher than for total abundance (r=0.95 vs r=0.94, respectively).

In October 1981, prions and Softplumaged Petrels were clumped at 15.1 ^{o}C. On the same cruise, prions, Greater Shearwaters, Whitechinned Petrels and Softplumaged Petrels were abundant at 19-20 ^{o}C, north of the main concentrations of prions and Softplumaged Petrels. For cruises where the model fit very well (i.e. r>0.70), one or two, but not always the same, species or diet-classes drove the model. Generally, when prions, Softplumaged and Whitechinned petrels or Blackbrowed Albatrosses were present in high abundances (relative to their mean abundances), and these birds were clumped together, the model produced middle to high correlation coefficients (i.e. r > 0.40).

Species which did not fit the model

During January 1980, certain species which did not fit the model reduced correlations between SST and the model driver species prions, Softplumaged Petrels and Wandering Albatrosses (r=0.55 vs r=0.40, Table 8). Bird variables which did not fit the model only reduced the r value by 0.01 in November 1981. In October 1981, plankton-eating birds so outnumbered other species that, in the equation for total abundance, the outliers (squid-, and mixed-diet species) had an r=-0.19 but did not effect the model fit. In October 1981, at the AGF, the species which at other times fit the model poorly gave a fit of r=0.34 and the planktivores were the outlier species, with an r=0.15. During September 1980, Blue, Whitechinned and Kerguelen petrels did not fit well, r=0.04, but only reduced the model fit for total abundance by 0.01 (Table 8).

The influence of weather upon seabird distribution

I considered the additional influence of macro-scale weather patterns on seabird abundance. Weather, barometric pressure and wind strength were more important in regression equations along single cruise tracks than at zonal scales (Table 6). For some cruises, temperature variables accounted for 20-30% of the variance and the addition of weather variables increased the total variance explained by another 5-10 %. This indicates a complex interaction effect between weather and sea upon seabird abundance. The direct influence of weather on biological populations is due to the cumulative effect of several meteorological events over longer time and space scales than my data represent (Steele 1978, 1981). Sometimes good weather contributed to increased seabird numbers, and at other times bad weather did so (Table 6).

Barometric pressure and the build-up and drop-off of winds are certainly non-linear phenomena. The relationship among weather variables was inconsistent. The average weather system passes south of Africa in four to five days, which is the duration of Prince Edward Islands cruises. Consequently, the influence on seabird abundance of weather cannot be adequately tested on single cruises. Time series data at a fixed point are needed for this. The influence of weather on seabird abundance is highly stochastic when data such as these are analysed.

Table 8. Model driver species and other species' correlation coefficients between seabird abundance and SST for selected single cruise tracks between Marion Island and Cape Town during 1979-1982

Cruise (Month)	Front	original r tot	driver r	suppressor r
Spring				
1a(9)	STC	0.43	PAC[1],HC[2] (0.41)	CF+MF(0.28)
4a(9)	STC	0.91	PAC,DM[3],PTM[4] (0.92)	HC,PRA[5],PTB[6] (0.04)
9a(10)	STC	0.79	PF(0.79)	CF+MF(-0.19)
9a(10)	AGF	0.33	CF+MF(0.34)	PF(0.15)
9b(11)	AGF	0.94	ST[7] (0.95)	
Summer				
2b(2)	STC	0.40	PAC,DE,PTM(0.55)	PUGA[8] (-0.43)
3a(2)	STC	0.43	PF+MF(0.41)	CF(0.35)FF(-0.05)
3b(3)	STC	0.61	PF(0.54)CF(0.51)	MF(0.36)FF(0.02)
6a(2)	STC	0.70	PF(0.56)MF(0.50)	FF(-0.06)
6b(3)	SAF	0.45	PF+MF(0.54)	CF(0.20)FF(-0.45)

1. prions, 2. Blue petrel, 3. Blackbrowed albatross, 4. Softplumaged petrel, 5. Whitechinned petrel, 6. Kerguelen petrel, 7. terns, 8. Great Shearwater

Discussion

Seabirds at sea appear to use habitat cues (e.g. SST) to identify different oceanic zones, or the fronts between them. Two oceanographic determinants of seabird distribution are indicated by two patterns: 1) correlations between each zones' avifauna and a specific set of conditions, and 2) within each zone, correlations between birds and certain 'attractive' fronts. The sub-tropical, sub-Antarctic and Antarctic oceanic zones represent three discrete steps in an environmental gradient, which, when represented by air-sea temperatures, correlates with the zonation of the avifauna. Analysis of seabird distribution for the whole study area reflected pattern 1, above. Seabird distribution by zone reflected pattern 1, while aggregations of birds within the zone near fronts reflected pattern 2, above.

South Atlantic and Antarctic pelagic fishes (Myctophidae) are distributed in response to temperature-salinity zonation and to disjunct areas of high primary production (Hulley, 1981; Targett, 1981). Disjunct distributions in response to meso-scale features have recently been confirmed in the Southern Ocean for cephalopods (Brandt, 1983) and zooplankton (Tranter et al., 1983 a,b). It is presumed that cephalopod and zooplankton distributions reflect macro-scale patterns of primary production in the Southern Ocean (Deacon, 1982). The Sub-tropical Convergence zone and the Antarctic water zone (> 50°S) support the highest measured values of primary production in the study area (Holm-Hansen et al., 1977; El-Sayed, 1978). Accordingly, squid-eating seabirds correlated with sub-tropical temperatures where squid are expected to be most abundant (Iverson, 1977). Planktivorous seabirds correlated with the STC zone temperatures, where primary production is relatively

highest and with cold temperatures of the Antarctic zone (Section 5.2.1), probably in response to the great abundance of krill (Euphasiacea) (Tranter, 1982; Weber and El-Sayed, 1985).

Seabirds flying between Africa and the Prince Edward Islands during spring were likely to be heading back to their sub-Antarctic breeding sites. Correlations between seabird abundance and cold temperatures suggest that seabirds followed a cold gradient towards the sub-Antarctic zone (Table 6). Associations in autumn between squid-eating seabirds and warm temperatures suggest that, as they dispersed from their breeding sites, they sought warmer sub-tropical water. The species of this diet-class, in particular, move nearer to Africa when not actively breeding (Abrams and Griffiths, 1981; Abrams, 1983). But these interpretations only account for a portion of the variation in seabird abundance because univariate regression models can not explain completely the movements of birds in transit; terrestrial bird navigation and homing involve a variety of environmental cues which are used from time to time by birds to orientate (Baker, 1978).

This study showed that as much as 30-40% of the variation in seabird abundance could be associated with the Africa-Antarctica environmental gradient (i.e. pattern 1 above, latitudinal zonation of the avifauna). Within habitat zones, these relationships reached high relative measures of association (i.e. up to 80% in terms of this seabird-SST model). Correlations of seabirds in nearshore areas with habitat variables which indicate fronts explained much smaller proportions of the variation of bird abundance (Abrams and Griffiths, 1981; Kinder et al., 1983). The extensive data herein enabled me to resolve and compare spatial and temporal scales,

which, when enhanced by the use of non-linear regression, explained a greater proportion of the variation in seabird distribution than previous studies. Modelling changes in terrestrial bird abundance along an environmental gradient was also most successful when the relationship was treated as non-linear (Meents et al., 1983).

Equation (1) is particularly sensitive to seabird abundance (P1) and the degree of resolution of SST (P3), i.e. sampling frequency along environmental gradient. Where the sea-surface temperature measurements approximated real-time and distance changes at sea, i.e. a continuum, the curve fitting proceeded more easily than where data resolved 0.5-1.0^{o}C temperature intervals. This must be kept in mind when considering the interpretation of these results. The positions and SST signatures of the fronts vary and the oceanographic data resolution available varied considerably from cruise to cruise. The STC and SAF are pushed south during summer by increased flow in the Agulhas Current (Clifford, 1983). This means that warmer conditions occur in higher latitudes during summer. Warming through spring of the SST's to which birds were attracted may reflect the change in, or broadening of, the location of the STC zone. The SST gradient at fronts during autumn may be less distinct than during other seasons, hence the poor model fits during autumn because the fronts were less attractive to the birds. Of the 24 cruises between Cape Town and 45 ^{o}S between April 1979 and April 1982, i.e. 60 crossings of the AGF, STC and SAF, 34 crossings were unresolved by oceanographic data or were of no interest to the birds. The causes of poor fits to the model may be poor data or random seabird distribution. The oceanographic analyses necessary to resolve this question and to discuss the dynamics of each front are beyond the scope of this

paper, but it is from such analyses that we might confirm how and why birds are attracted to particular oceanic features.

Total abundance and selected single species should both be used as dependent variables in modelling seabird-temperature associations. The results of the Gaussian-curve model were unequivocal when the model driver species were present in numbers >25. Unusually large numbers of terns drove the model in November 1981 (r=0.94), whereas prions were the model driver most often, as in October 1981 (r=0.79), which typifies the difficulty in modelling seabird-habitat relationships. Use of single species alone as indicators is not advisable. Due to the very large variances in pelagic counts of seabirds, i.e. the large variances characteristic of the model parameter Pl, it seems unlikely that generalisations can be made a priori about the range of abundances useful in predictive modelling. Rather, interpretation of each case must be based on oceanic conditions during the cruise from which the bird data come.

The relatively high energy per unit time required by planktivores implies that they be consistently oriented with respect to prey location (Section 5.1.1). Planktivores at sea have been the seabirds most easily related to weather and sea-surface structure in the African sector of the Southern Ocean (Mendelsohn, 1981; Griffiths et al., 1982; Section 5.1.1). Planktivorous seabirds are probably the best indicator of prey availability in space and time scales of less than 360 km and a month, respectively. Planktivores and plankton show patchy distributions (Tranter, 1982; Tranter et al., 1983 a; Weber and El-Sayed, in press; Section 5.2.1), perhaps produced by the meso-scale variability of Southern Ocean water structure, i.e. frontal meanders and

cold-core rings averaging 180-360 km diameter and a month to move across one diameter (Steele, 1978; Lutjeharms, 1981; Hofmann et al., in press).

The stochastic influence of weather on bird abundance makes it difficult to use weather in a deterministic model of seabird-habitat associations. Seabirds may use weather as a macro-scale orientation cue since the latitudinal zones of the Southern Ocean have different climates. The use of regression techniques to unravel seabird-weather associations is of dubious value.

Conclusion

This study has constructed the hypothesis that in the region of an oceanic front, seabirds clump at a sea-surface temperature signature of the front. The validity of the model of seabird-front association requires testing of the hypothesis that in the vicinity of fronts, i.e. 200-540 km, consistently high proportions of variation of seabird abundance can be explained by a Gaussian curvilinear correlation with SST. The relevance of SST data as a signature of the surface expression of a thermohaline front must be confirmed by vertical and horizontal hydrological analyses

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APPENDIX 1. (a) Research cruises of the M.V. S.A. Agulhas in the African sector of the Southern Ocean, April 1979-May 1982. (b) cruises from which data were taken for the curvilinear model of seabird - SST associations. Cruises for which oceanographic data were analysed by Lutjeharms and Valentine(*).

(a)

DATE		DESTINATION
30-04-79	14-05-79	SOUTH TO 48° S, GOUGH
23-05-79	13-06-79	MARION
18-07-79	05-08-79	GOUGH, BOUVET, ICE
07-09-79	24-09-79	MARION
26-10-79	16-11-79	GOUGH
05-01-80	10-02-80	S A N A E
29-02-80	01-04-80	PRE-FIBEX (BIOMASS)
11-06-80	13-06-80	MARION
04-09-80	24-09-80	MARION
16-10-80	24-10-80	GOUGH
31-12-80	28-01-81	S A N A E
11-02-81	19-03-81	FIBEX (BIOMASS)
18-04-81	12-05-81	MARION
04-06-81	12-06-81	MARION
16-10-81	25-11-81	MARION
17-04-82	25-05-82	MARION

(b)

	DESTINATION		MONTH	NUMBER FRONTS + LEG IDENTIFIER Out (a)	In (b)
1	MARION	1979	9	1	2
2	SANAE	1980	1-2	2*	1*
3	PREFIBEX	1980	2-3	2	1*
4	MARION	1980	9	1*	0*
5	SANAE	1981	1	1*	2*
6	FIBEX	1981	2-3	2*	2*
7	MARION	1981	4-5	0	2
8	MARION	1981	6	1	3
9	MARION	1981	10-11	1	2
10	MARION	1982	4-5	1	0

Appendix 2. Principal food-type and feeding-method class, body-weights and percentage abundance (numbers of individuals) of species observed in the African sector of the Southern Ocean for 1979-80 and 1980-81. Food and feeding classification based on data in Ashmole (1971) and unpublished records taken from the FitzPatrick Institute which also maintains records of bird weights

Food-type	Feeding-method	Species	Body-weight (kg)	Abundance 1979-1980	Abundance 1980-1981
Plankton	Surface-filter	Pachyptila spp, prions	0.15	33.6	50.7
"	Surface-seize/scavenge	Halobaena caerulea, Blue Petrel	0.21	13.2	4.9
"	Pursuit-plunge	Puffinus puffinus, Manx Shearwater	0.48	<0.1	0
"	Dip/patter	Oceanites oceanicus, Wilson's Stormpetrel	0.04	0.3	0.4
"	Dip/patter	Oceanodroma leucorhoa, Leach's Stormpetrel	0.05	0.1	0.1
"	Dip/patter	Fregetta tropica, Blackbellied Stormpetrel	0.06	0.3	0.3
"	Dip/patter	Fregetta grallaria, Whitebellied Stormpetrel	0.06	<0.1	<0.1
"	Dip/patter	Garrodia nereis, Greyrumped Stormpetrel	0.03	0	<0.1
"	Dip/patter	Pelagodroma marina, Whitefaced Stormpetrel	0.03	<0.1	0
"	Dip/patter	Hydrobates pelagicus, European Stormpetrel	0.04	0.1	<0.1
"	Pursuit-plunge	Pelecanoides spp., divingpetrels	0.12	0.4	0.5
"	Dip-patter	Phalaropus fulicarius, Grey Phalarope	0.03	0.1	<0.1

Cephalopods	Surface-seize/scavenge	Diomedea exulans, Wandering Albatross	8.60	0.7	0.93
"	Surface-seize/scavenge	Diomedea melanophris, Blackbrowed Albatross	3.50	0.8	1.31
"	Surface-seize/scavenge	Diomedea chrysostoma, Greyheaded Albatross	3.60	0.3	0.3
"	Surface-seize/scavenge	Diomedea chlororhynchos, Yellownosed Albatross	2.00	0.2	0.3
"	Surface-seize/scavenge	Diomedea cauta, Shy Albatross	4.10	0.3	0.2
"	Surface-seize/scavenge	Phoebetria fusca, Sooty Albatross	2.50	0.3	0.8
"	Surface-seize/scavenge	Phoebetria palpebrata, Lightmantled Sooty Albatross	2.70	0.4	0.3
"	Surface-seize/scavenge	Fulmarus glacialoides, Antarctic Fulmar	1.00	0.4	0.6
"	Surface-seize/scavenge	Daption capense, Pintado Petrel	0.45	0.6	0.7
"	Surface-seize/scavenge	Pterodroma macroptera, Greatwinged Petrel	0.58	1.3	1.0
"	Surface-seize/scavenge	Pterodroma lessonii, Whiteheaded Petrel	0.75	1.1	0.7
"	Surface-seize/scavenge	Pterodroma incerta, Atlantic Petrel	0.52	0.4	0.6
"	Surface-seize/scavenge	Procellaria aequinoctialis, Whitechinned Petrel	1.21	1.4	3.8
"	Surface-seize/scavenge	Procellaria cinerea, Grey Petrel	1.03	0.2	0.1
"	Pursuit-plunge	Puffinus gravis, Great Shearwater	0.95	14.8	3.5

Fish	Surface-seize/scavenge	Calonectris diomedea, Cory's Shearwater	0.96	0.1	0.9
"	Pursuit-plunge	Puffinus griseus, Sooty Shearwater	0.79	1.0	7.4
"	Dip-patter	Sterna vittata, Antarctic Tern	0.14	<0.1	2.8
"	Dip-patter	Sterna paradisaea, Arctic Tern	0.13	1.3	0.4
"	Plunge	Sula capensis, Cape Gannet	2.59	0	<0.1
"	Surface-seize/scavenge	Puffinus assimilis, Little Shearwater	0.23	0.9	2.3
Mixed	Surface-seize/scavenge	Macronectes giganteus, Southern Giant Petrel	4.10	0.3	0.2
"	Surface-seize/scavenge	Macronectes halli, Northern Giant Petrel	5.20	0.3	0.1
"	Surface-seize/scavenge	Thalassoica antarctica, Antarctic Petrel	0.70	6.6	1.6
"	Surface-seize/scavenge	Pagodroma nivea, Snow Petrel	0.30	1.6	0.5
"	Surface-seize/scavenge	Pterodroma brevirostris, Kerguelen Petrel	0.33	7.0	4.3
"	Surface-seize/scavenge	Pterodroma mollis, Softplumaged Petrel	0.31	6.8	7.0
"	Piracy	Catharacta antarctica, Subantarctic Skua	1.63	<0.1	<0.1
"	Piracy	Catharacta maccormicki, MacCormick's Skua	1.26	<0.1	<0.1
"	Piracy	Stercorarius pomarinus, Pomarine Skua	0.67	<0.1	<0.1
"	Piracy	Stercorarius parasiticus, Arctic Skua	0.53	<0.1	<0.1
"	Piracy	Larus dominicanus, Southern Blackbacked Gull	1.00	0	<0.1
"	Piracy	Stercorarius longicaudus, Longtailed Skua	0.29	<0.1	<0.1

APPENDIX 3. Goodness of fit of curvilinear model (r), sample size (n), and Gaussian curve parameters (P1,P2,P3) for total seabird abundance by SST across fronts in the African sector of the Southern Ocean, Sept 1979 to May 1982. Crossings are presented for which data permitted a fit of the curvilinear model (26 of 60 possible crossings, reference cruise and month to Appendix 1).

	Cruise (Month)	Front	r	n	curve perameters (P1)	(P2)	(P3)
Spring	1a(9)	STC	0.43	39	118.0	12.4	0.240
	1b(9)	AGF	0.72	8	33.4	15.8	0.067
	1b(9)	SAF	0.25	34	5.7	8.2	1.800
	4a(9)	STC	0.91	81	252.0	13.4	1.360
	9a(10)	STC	0.79	36	253.0	15.1	0.017
	9a(10)	AGF	0.33	44	16.8	20.1	0.230
	9b(11)	AGF	0.94	78	325.0	18.1	0.013
Summer	5a(1)	SAF	0.21	42	3.9	7.2	2.210
	5b(1)	STC	0.35	37	16.6	17.1	1.400
	5b(1)	AGF	0.35	35	18.2	20.7	0.001
	2a(1)	STC	0.15	180	23.7	14.7	16.700
	2b(2)	AGF	0.40	28	11.5	20.1	0.410
	3a(2)	STC	0.43	98	50.4	13.4	3.210
	3a(2)	SAF	0.95	37	441.7	9.6	0.008
	3b(3)	STC	0.61	56	39.4	17.4	0.330
	6a(2)	AGF	0.37	64	3.6	20.6	0.036
	6a(2)	STC	0.70	52	13.5	19.2	4.980
	6b(3)	AGF	0.26	80	90.1	21.1	0.080
	6b(3)	SAF	0.45	30	15.6	8.5	0.130
Autumn/ Winter	7b(5)	STC	0.26	28	9.1	17.9	0.310
	7b(5)	SAF	0.34	26	9.8	9.2	0.450
	10a(4)	STC	0.43	70	55.6	15.5	7.000
	8a(6)	STC	0.23	76	19.3	12.5	20.000
	8b(6)	STC	0.33	13	16.1	13.6	0.200
	8b(6)	AGF	0.50	38	26.0	12.3	20.000
	8b(6)	SAF	0.78	25	26.2	8.7	0.720

5.1.3. FIBEX Correspondence Analysis

Relationships of pelagic seabirds with the Southern Ocean environment assessed by Correspondence Analyses

Abstract. A descriptive, ordination procedure, Correspondence Analysis, is used to characterize the changes in abundance of four Southern Ocean seabird diet classes along the Africa - Antarctica environmental gradient. The analysis suggests that the relationship between planktivores and piscivores with sea-surface temperature follows a quadratic or bell-shaped function. The relationship between squid-eating and mixed-diet seabirds with windspeed may follow an increasing function with an asymptote.

Spatio-temporal changes in pelagic seabird assemblages probably reflect changes in the dispersion of prey stocks (Croxall, 1984). Direct observations of seabird-prey interactions are too rare to allow modelling on that basis alone (Griffiths, 1983). Construction of a deterministic model of seabird-habitat relationships, which is linked to a similar prey-habitat interaction model, seems the most practical approach to the question of whether or not monitoring pelagic seabirds can be useful in the management of pelagic prey stocks. Such a model requires an understanding of the multiple environmental cues used by seabirds to 'read' their habitat for purposes of long-range navigation (Baker, 1978) between areas of high prey density and seabird breeding colonies.

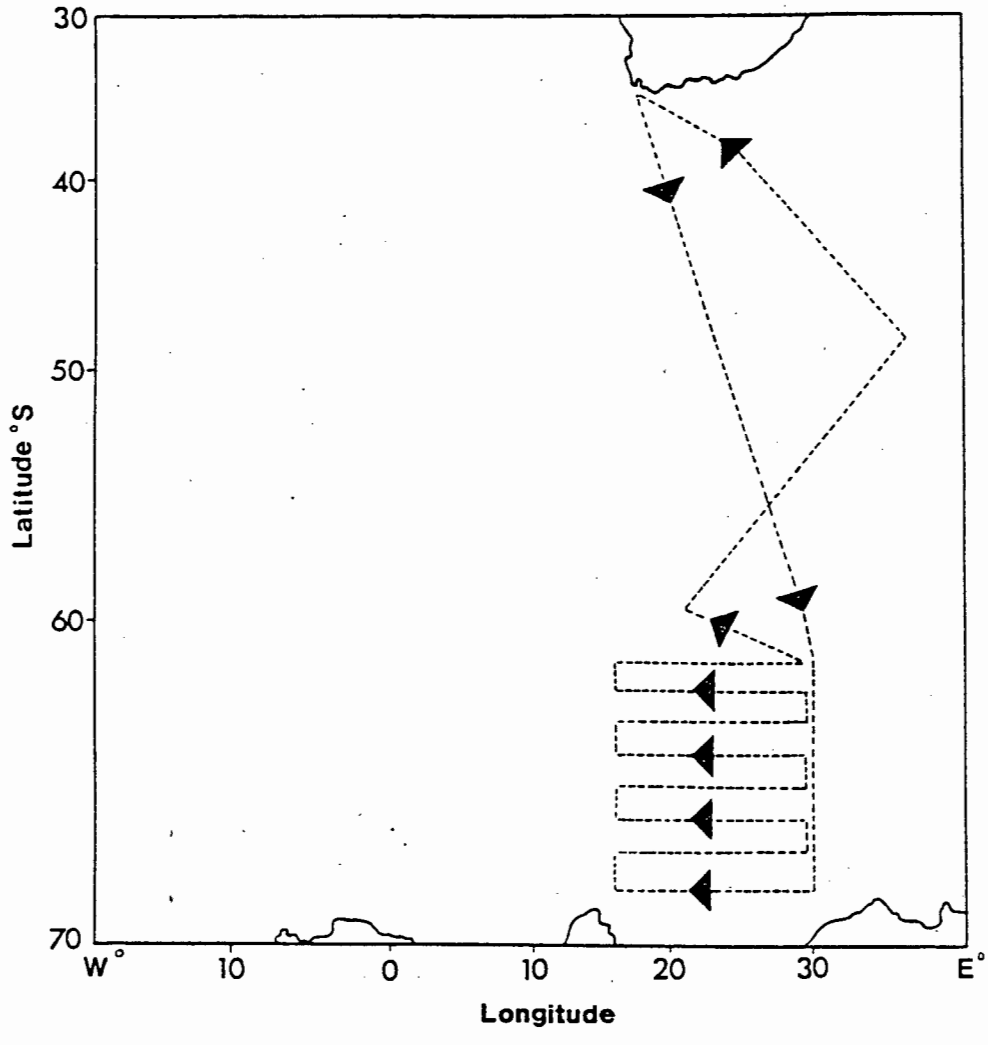
Seabird distribution in deep-sea areas has been related qualitatively to patterns of sea temperature, salinity and weather (Pocklington, 1979). Areas of peak seabird density coincide with oceanic areas reported to contain concentrations of food (Griffiths et al., 1982; Section 5.1.1). If these areas can be recognized by simple environmental parameters then a descriptive model of seabird-habitat-prey relationships can be developed.

Linear regression techniques applied to seabird-habitat interactions have been insufficient, suggesting that models must include non-linear relationships between seabird abundance and, for example, sea-surface temperature (Section 5.1.2; Section 5.2.1). This paper reports preliminary efforts to use Correspondence Analysis to qualify the relationships of seabird abundance with temperature, wind strength and weather parameters. The nature of non-linear regression equations which may fit a deterministic model can be explored in this manner.

Methods

Data on seabird distribution and environmental variables were collected aboard the M.V. S.A. Agulhas during 16 February to 10 March, 1981, in an area bounded by 59° and 69°S and 15° and 30°E and between this area and Cape Town as part of the First International BIOMASS Experiment (FIBEX) (Fig.1). All birds flying past and passed by, the moving ship (mean speed = 23.4km h^{-1}) in a 1km-wide transect were recorded as described by Griffiths (1981), during 1445 10-minute seabird observations (hereinafter referred to as stations).

Fig. 1. Study area, African sector of the Southern Ocean showing FIBEX cruise track.



The predictability of the abundance of seabirds in four diet classes (plankton, squid, fish, mixed) in relation to environmental features was assessed at oceanic and regional scales by identifying the relative strengths of seabird associations with air temperature (AIR), water temperature (WAT), barometric pressure (BAR), wind strength on Beaufort scale (WIND) and weather (WEATH) coded from 1 (clear sky) to 6 (storm with rain or snow).

Each of the variables (four seabird and five environmental) was categorized on a three-point scale (High, Medium, Low) with cutpoints chosen in such a way so that as close as possible to 1/3 of the 1445 data points for that variable fell into each category. The exception was seabird diet group 'fish feeders', which could only be categorized as High and Low. The nine original variables then became 15 environmental and 11 seabird variables. A 15 x 11 matrix, $\underline{X}$, was produced with element $\underline{X}ij$ in row i and column j of $\underline{X}$ being the number of times environmental variable i and seabird group variable j cooccurred at the 1445 stations.

The matrix $\underline{X}$ was then subjected to Correspondence Analysis, a data analytic technique which displays the most important relationship between the rows and columns of the matrix (in this case the relationship between seabird groups and the environmental variables) and orders them from most to least important in a series of axes (Benzecri et al., 1973; Greenacre, 1978, 1984, Greenacre and Underhill, 1982). Plots can be made of pairs of axes, and the proportion of the information in the data matrix explained by each axis is provided as a measure of confidence in the patterns resolved. The relative strength and general curvilinear form of the associations among the variables can be deduced from the geometrical relationship of the variable vectors, within the limits of the three-point scale.

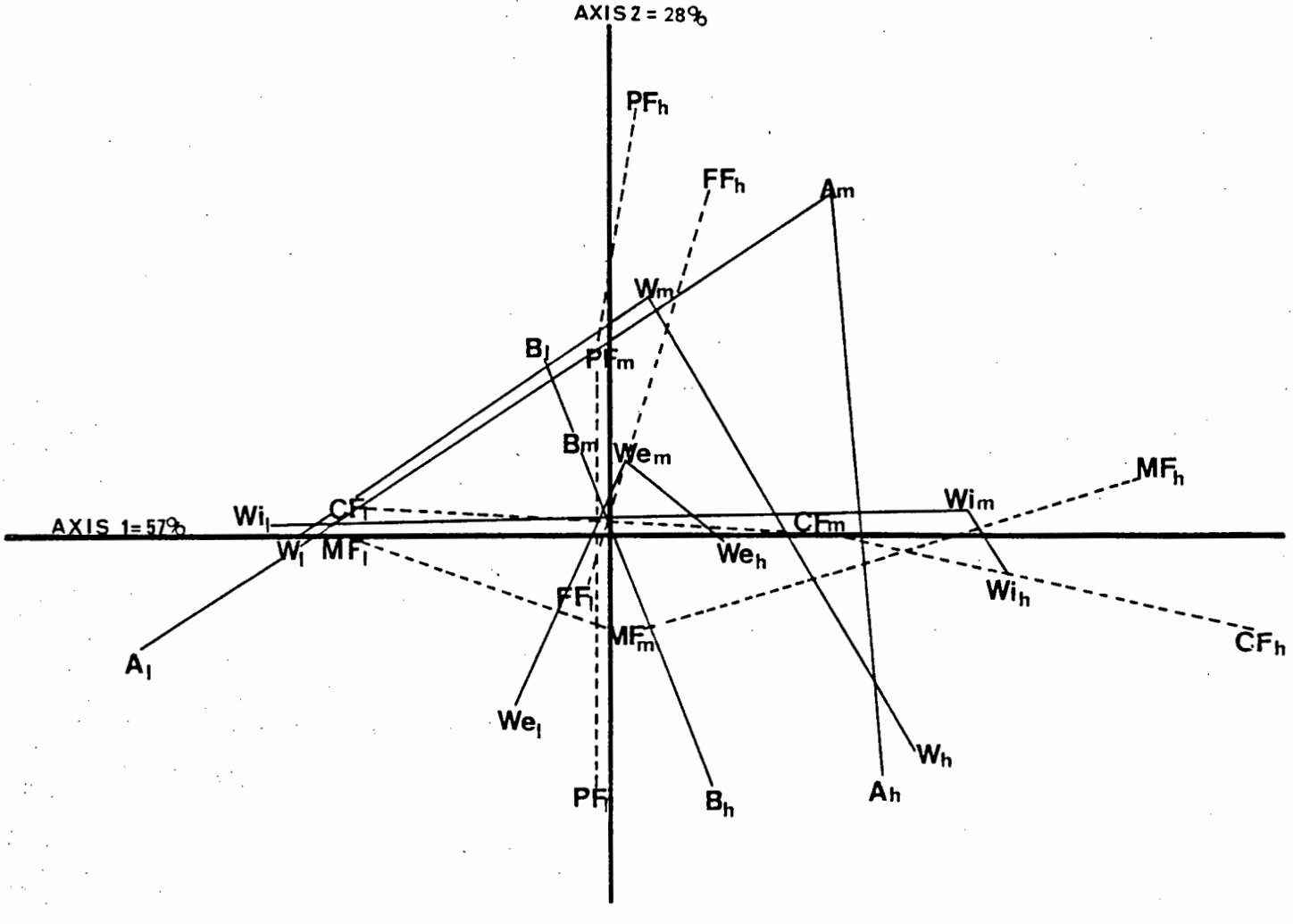
Results and Discussion

Seabirds which take principally cephalopods or mixed diets occur on Correspondence Analysis axis 1, which accounts for 58% of the total information content of the data matrix (Fig. 2). Species which generally feed on plankton and fish occur on CA axis 2, which accounts for a further 27% of the data matrix. Thus, the first two axes account for 85% of the information contained in the data. Species-classes which sometimes occurred in large flocks, planktivores and piscivores, are independent (in terms of variables influencing their abundance) from the distribution of species which contribute to avifaunal diversity (corroborated by Griffiths et al., 1982).

Water and air temperature covary but define a non-linear trend across CA axes 1 and 2 (Fig. 2). That temperature has an association with seabird abundance is clear from previous linear analyses, but the nature of the relationship requires a measure of confidence (Abrams and Griffiths, 1981; Section 5.1.2). Moreover, an explanation of the weak contributions of weather and barometric pressure to strictly linear regression equations is made clear by the CA results. Weather and wind strength show non-linear associations to bird variables.

The CA results provide graphical description of what have been statistically weak, but intuitively meaningful, seabird-habitat correlations. Seabird species which wander widely, and are predominant in the sub-tropical region (e.g. albatrosses and large petrels), coincide with the warm part of the air and water temperature curve (Abrams and Griffiths, 1981, Griffiths et al., 1982, Section 5.1.2).

Fig. 2. Variability in seabird abundance (dashed lines; PF-plankton eating species; CF-squid eating species; FF-fish eating species; MF-mixed diet species), compared with variability in physical habitat parameters (solid lines; B-barometric pressure; A-air temperature; W-sea-surface temperature; Wi-windspeed; We-weather). The ranges for the variables are grouped as low (L) to high (H).



Species that dominate the sub-Antarctic and Antarctic seas, feeding mainly on plankton and fish (e.g. prions, terns, small shearwaters and petrels), are most abundant in association with sea-surface temperatures in the middle of the range of the areas covered by the FIBEX cruise (~5-13°C). The CA suggests that the abundance of plankton- and fish-eating birds may be related to temperature by a nonlinear function with a single mode (Fig. 3a,b).

Abrams and Griffiths (1981) and Griffiths et al. (1982) found relatively few of the planktivores from the Southern Ocean in the warm sub-tropical region. The north-south zonation of certain seabird species suggests that the Africa-Antarctica temperature gradient may be useful to the birds for navigation or orientation. Plantivores and piscivores dominated the avifauna in high latitudes (>50°S) and their abundance apparently correlated with patches of relatively warm upwelled water in the vicinity of the "Antarctic Divergence." The curvilinear nature of seabird-temperature associations has not been easy to model (Section 5.1.2).

Overcast, dry weather corresponds with the moderate temperatures in the CA results, which are conditions associated with relatively high abundances of planktivores and piscivores. This concurs with results from linear analyses which suggested that piscivores avoid bad weather and strong winds (Sections 5.1.2, 5.2.1). The results of correlations between planktivore abundance and weather in Section 5.1.2 are inconsistent, which suggested that there was a curvilinear relationship involved. This paper supports that suspicion.

This study shows an association between low planktivore abundance and clear weather with high barometric pressure (Fig. 2). There

may be a tendency among these species to leave an area of good weather in anticipation of incoming bad weather, as indicated by a correspondence between low barometric pressure (which accompanies a cold front) and planktivore abundance (Fig. 2). Mendelsohn (1981) found that prions (Pachyptila) avoid bad weather and proposed this to be because sea-surface turbulence disperses plankton otherwise concentrated in the euphotic zone near the surface, during relative calm (Tranter 1977).

Nisbet and Drury (1968) consider that the more powerful correlates of bird migration density are parameters associated with the weather at the migrator's destination, implying that birds are adapted more to weather prediction than to tolerance of current conditions. Unfortunately, this study does not allow us to determine whether the planktivores are associated with the leading, or the trailing edge of a weather system, but we suspect the birds can so differentiate. Further, carefully designed data collection (i.e. time-series analysis) is necessary to define the precise nature of the relationship of flocking species with the passage of weather systems.

Sections 5.1.2 and 5.2.1 demonstrate that cephalopod- and mixed diet feeding species pay only limited attention to weather, as might be expected for widely dispersed, meandering species which can go relatively long periods between meals (Section 5.1.1). CA axis 1 suggests that squid-eating and mixed-diet seabirds are associated with moderate to high wind speeds (4-10 Beaufort scale, Fig. 2). Wandering Albatross (Diomedea exulans) in the Southern Ocean are associated with boundary areas between these wind speeds and low wind speeds (Abrams et al., 1981). The birds use wind, but do not seem constrained by it. The CA suggests that the abundance of seabirds which take principally squid and mixed-diets is related to wind speed by a non-linear function with an asymptote (Fig. 3 c and d).

Conclusion

The use of Correspondence Analysis to explore the nature of seabird-habitat associations has provided a measure of confidence that seabird-habitat relationships require non-linear modelling. In the case of temperature the equation appears to be quadratic or possibly bell-shaped. In the case of windspeed, the equation appears to increase to an asymptote.

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5.2. Meso-scale seabird distributions

Pelagic seabird distribution and abundance in relation to meso-scale variability in marine habitat structure

Oceanographic determinants of the distribution and abundance of pelagic seabirds operate on scales of biogeographical zones (macro-scale) and over areas $<3 \times 10^3$ km^2 (meso-scale). Section 5.2.1 shows that the absolute numbers and species composition of the avifauna associated with macro-scale zones are only general trends, and that within these zones are finer scale distributions. Sections 5.2.2 to 5.2.3 show that these meso-scale distributions are associated with meso-scale oceanic flow variability. Moreover, the distribution of the seabirds in both of these studies correlates with the distribution of potential prey. Section 5.2.4 assesses statistically the relationship between seabird assemblages and particular habitat-types and the hydrological processes which generate meso-scale habitat variability.

5.2.1. FIBEX seabirds

Distribution of seabirds in the African sector of FIBEX

The paper presents a quantitative account of the abundance of seabirds (excluding penguins) in relation to environmental features in a small area of the southern Indian Ocean. Plankton-eating birds were abundant. Piscivorous birds were less numerous, but their biomass was slightly higher than that of the planktivores. Cephalopod-eaters and species in a mixed-diet class were widespread, but not as abundant as either planktivores or piscivores. Planktivores were most abundant in a narrow latitudinal band at 61-63^{o} S. High planktivore abundance was correlated positively (about 33 %) with relatively warm air and surface-water temperatures and low barometric pressure, and high piscivore abundance (about 32 %) with weak winds and cloudy to wet weather. The abundance of cephalopod-eaters correlated very poorly (about 4 %) with these variables.

Introduction

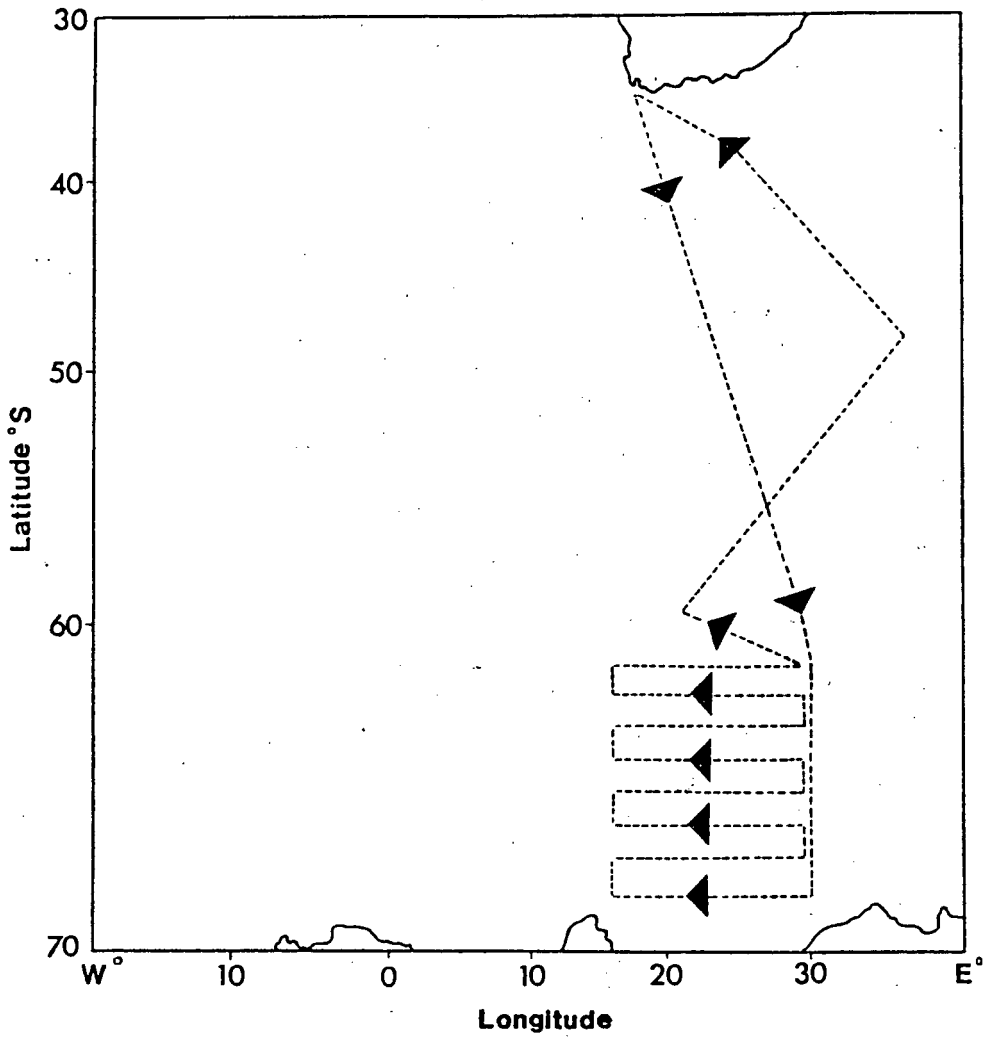
During the austral summer of 1980 - 1981, an international survey was carried out, as part of BIOMASS (Biological Investigations of Marine Antarctic Systems and Stocks), in order to gain information on the distribution and abundance of krill Euphausia superba and its predators in the Southern Ocean (Anon., 1977). The survey, known as FIBEX (First International BIOMASS Experiment), was made in areas believed to contain dense concentrations of krill (Mauchline, 1980).

This paper gives a preliminary account of the distribution of pelagic seabirds (excluding penguins because they are difficult to detect and count at sea) in the FIBEX sector of the southern Indian Ocean surveyed by South Africa. More particularly, the report deals with the abundance of seabirds in relation to selected environmental features, in a preliminary assessment of the usefulness of seabirds as indicators of peculiar oceanic biotopes and prey populations.

Materials and Methods

The M.V. S.A. Agulhas operated from 16 February to 10 March, 1981, in an area bounded by 59°and 69°S and 15°and 30°E (Fig. 1). All birds flying past, and passed by, the moving ship (mean speed = 23.4km h^{-1}) in a 1-km-wide transect were recorded as described by Griffiths (1981), during 585 10-minute seabird observations (referred to as stations). Barometric pressure, air and surface-water temperatures, wind strength (Beaufort scale) and weather (cloud cover and precipitation, scaled from 1 (clear) to 6 (storm)) were recorded at each station.

Fig. 1. Cruise track of the M.V. S.A. Agulhas in the South African sector of FIBEX in the southern Indian Ocean, 16 February to 10 March, 1981.



The avifauna was analysed according to species richness (BSR = total number of species), Shannon-Wiener diversity index (BSD = H $=-\sum p_i \log p_i$, where p_i is the proportion of the i^{th} species in the assemblage), abundance (number of individuals) and biomass (total live-weight of all birds) at each station in relation to four principal diet and four feeding-method categories (Appendix 1). Patterns of seabird dispersion were examined from computer-drawn maps, using the SOPS plotting programme (Abrams et al., 1981). Linear and stepwise multiple regression and factor analysis (PCA) were used to characterize relationships within the avifauna and between the birds and their environment. Linear correlation matrices, including all biotic and abiotic parameters, facilitate focusing on noteworthy patterns. Use of this technique does not imply tests of hypotheses, since inferential statistics require certain assumptions to be met which are not valid for these data. Multi-colinearity and non-normal distributions were adjusted when multiple regressions were calculated between diet groups and physical variables. These analyses are not, however, meant to be taken as inferential tests of hypotheses, but rather as characterizations of associations between seabirds and major enviromental features.

Results

Seabirds tended to be clumped (Fig. 2) in the area between 61-63° S, especially plankton-eaters (Fig. 3). During this study two species and 25 birds were recorded at an average observation station (Table 1). Planktivores (including krill eaters) contributed the greatest numbers of species and individuals per

Fig. 2. The distribution and mean abundance (no. individuals) of seabirds (excluding penguins) according to half-degree quadrates in the South African sector of FIBEX in the southern Indian Ocean, 16 February - 10 March, 1981.

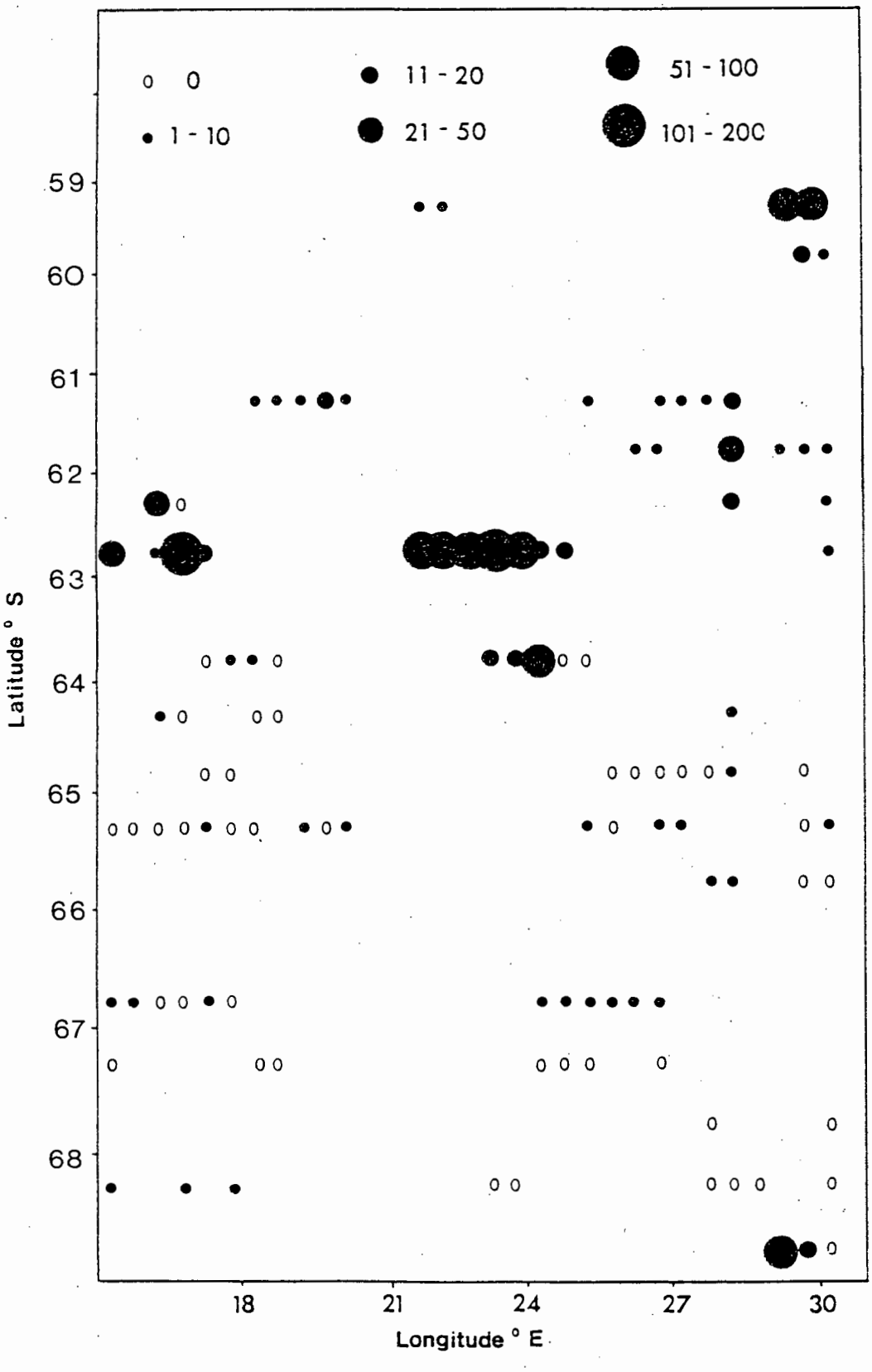


Fig. 3. The distribution and mean abundance (no. individuals) of plankton-eating seabirds (excluding penguins) according to half-degree quadrates in the South African sector of FIBEX in the southern Indian Ocean, 16 February - 10 March, 1981.

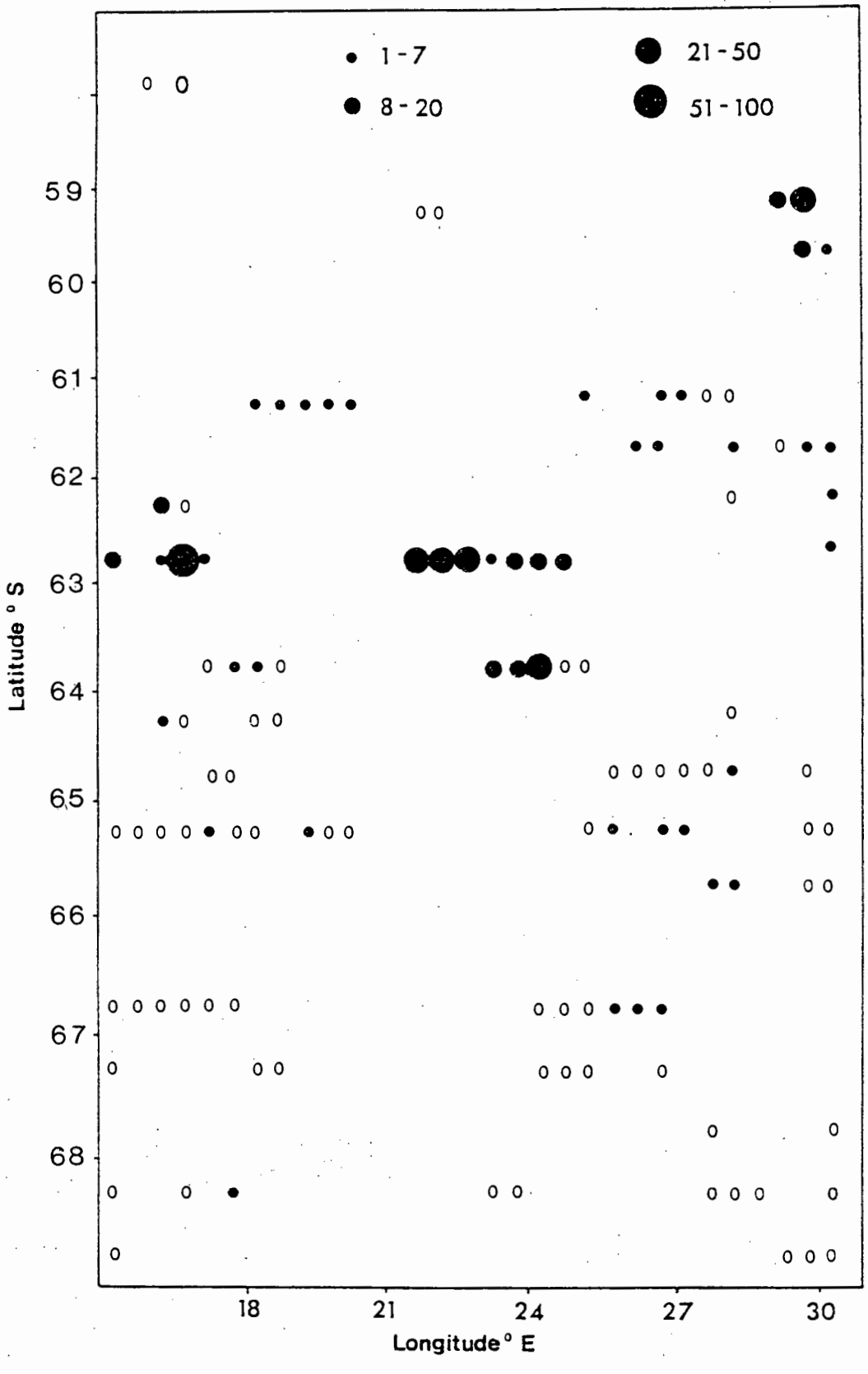


Fig. 4. The distribution and mean abundance (no. individuals) of fish-eating seabirds (excluding penguins) according to half-degree quadrates in the South African sector of FIBEX in the southern Indian Ocean, 16 February - 10 March, 1981.

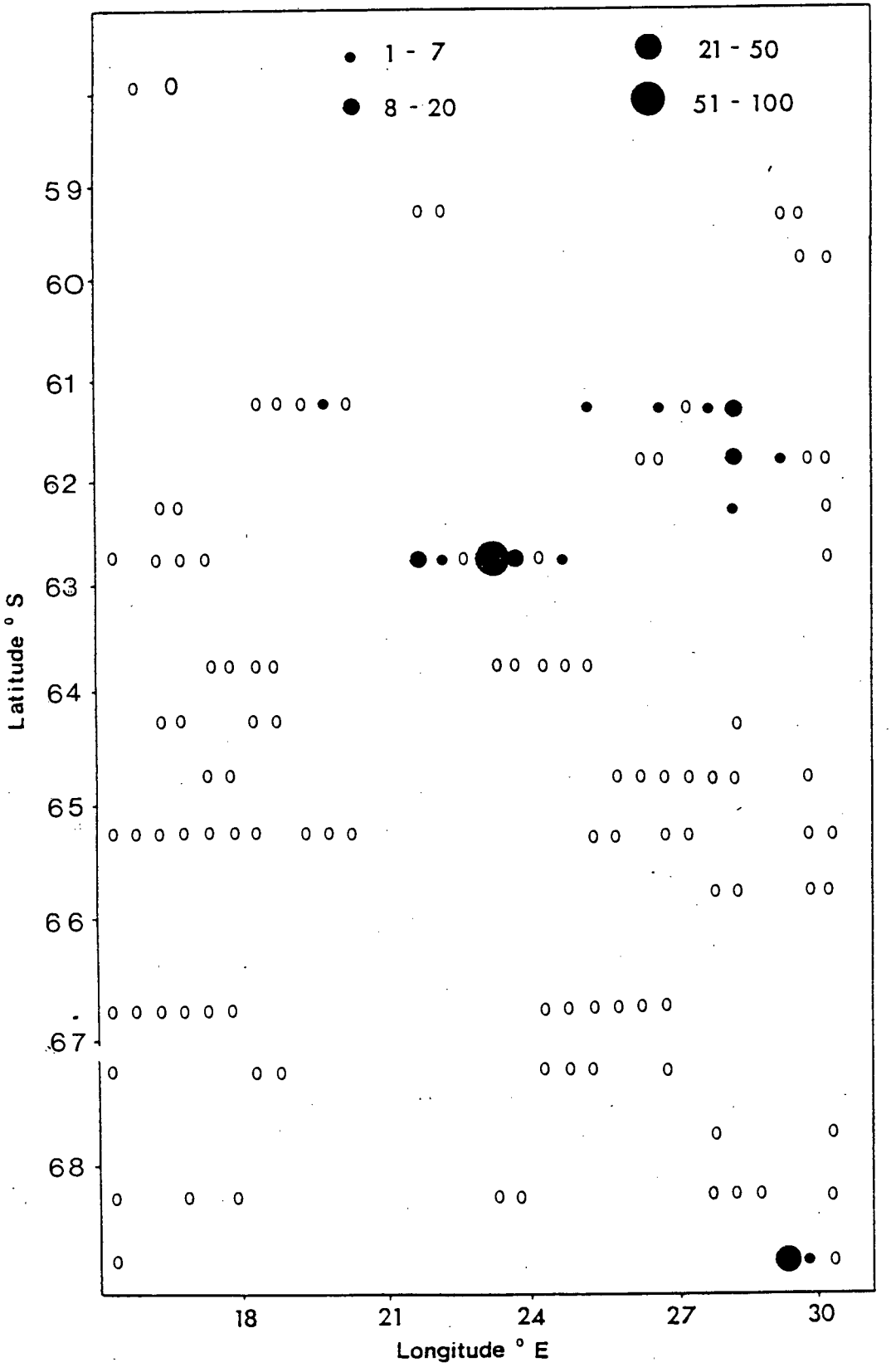


Table 1. Mean species richness (BSR), diversity (BSD), abundance (number of individuals) and biomass (kg live-weight) of seabirds (excluding penguins) at 585 stations in the South African sector of FIBEX in the southern Indian Ocean.

	BSR	BSD	Abundance	Biomass
Mean	2.01	0.44	25.24	7.82
S.D.	1.29	0.43	39.14	25.77
Range	0-7	0-1.83	0-1574	0-322.50
Total			15608	4657

Table 2. Mean abundance (number of individuals) of seabirds (excluding penguins) according to four principal food-type classes at 585 stations in the South African sector of FIBEX in the southern Indian Ocean.

	Food type			
	Plankton	Cephalopod	Fish	Mixed
Mean	16.44	0.69	6.62	1.49
S.D.	81.49	2.22	34.79	3.11
Range	0-1573	0-44	0-460	0-32

Table 3. Coefficients of correlation (r) between species richness (BSR), diversity (BSD), abundance (number of individuals) and biomass (kg live-weight), and food-type groups of seabirds (excluding penguins) at 585 stations in the South African sector of FIBEX in the southern Indian Ocean.

Food type	BSR	BSD	Abundance	Biomass
Plankton	0.526	0.230	0.826	0.521
Cephalopods	0.469	0.419	0.251	0.285
Fish	0.238	0.054	0.540	0.730
Mixed	0.454	0.408	0.306	0.084

Table 4. Coefficients of correlation (r) between food-type and feeding-method groups of seabirds (excluding pengiuns) at 585 stations in the South African sector of FIBEX in the southern Indian Ocean.

	Food type			
Feeding method	Plankton	Cephalopods	Fish	Mixed
Surface-seizing	0.398	0.422	- 0.053	0.613
Surface-filtering	0.945	0.156	0.202	0.048
Pursuit-plunging	0.246	0.002	0.906	- 0.136
Dipping/pattering	- 0.100	- 0.081	0.304	0.248

station (Tables 2 and 3). Although there were relatively few piscivorous species (Appendix 1), they were abundant and accounted for a biomass slightly higher than that of the planktivores. Cephalopod-eaters, and those species placed in a mixed-diet class (species not classifiable as either predominantly plankton-, cephalopod- or fish-eaters), were widespread, but not as abundant as either planktivores or piscivores (Tables 2 and 3). Correlations between the principal diet groups and the feeding methods used by the birds (Table 4) and between each of the four diet and feeding method groups separately (Tables 5 and 6) showed that there was no trend in co-occurrence between species belonging to different diet groups. Planktivores and piscivores co-occurred together but were not entirely coincident, in a narrow latitudinal band at 61-63^{o}S (Figs 3 and 4).

The abundance of planktivores and piscivores was correlated with 33 % and 32 %, respectively, of the variation of the physical parameters considered here; not more than 4 % of the variation of abundance of cephalopod-eaters was explained by these variables (Table 7). High planktivore abundance was associated with relatively warm air and surface-water temperatures and low barometric pressure. High planktivore abundance was also associated with cloudy to wet weather and relatively calm winds (Fig. 5). High piscivore abundance was associated with high barometric pressure, weak winds and cloudy weather (Table 7, Fig. 5). In addition to these primary biotic-abiotic associations, the various seabird diet groups were associated with other combinations of abiotic variables (Table 7).

Table 5. Coefficients of correlation (r) between food-type groups of seabirds (excluding penguins) at 585 stations in the South African sector of FIBEX in the southern Indian Ocean.

Food-type	Plankton	Cephalopods	Mixed
Cephalopods	0.132	1.000	
Fish	0.184	-0.037	1.000
Mixed	0.045	0.078	-0.021

Table 6. Coefficients of correlation (r) between feeding-method groups of seabirds (excluding penguins) at 585 stations in the South African sector of FIBEX in the southern Indian Ocean.

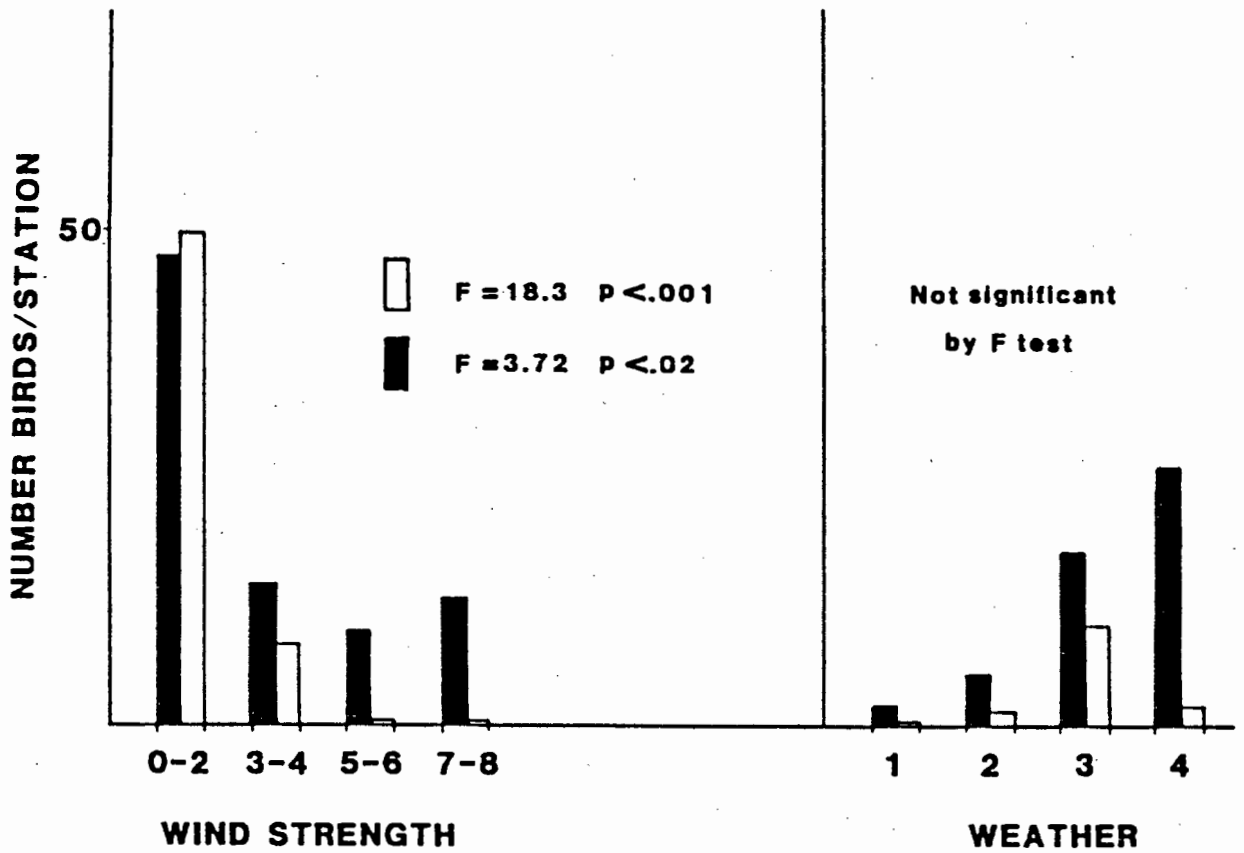
Feeding-method	Surface-filtering	Pursuit-plunging	Dipping/Pattering
Surface-seizing	0.240	-0.108	0.093
Surface-filtering	1.000		
Pursuit-plunging	0.287	1.000	
Dipping/Pattering	-0.171	-0.081	1.000

Table 7. Coefficients of determination (R^2) between abundance (no. individual birds) of four food-type groups of seabirds (excluding penguins) and subsets of five physical variables (BAR = barometric pressure, AIR = air temperature, WAT = surface-water temperature, WIN = wind strength, WEA = weather) in the South African sector of FIBEX in the southern Indian Ocean. The directional influence of each variable in the regression equation is indicated (+, -).

Physical variables	Food-type			
	Plankton	Cephalopods	Fish	Mixed
BAR	-	-		
AIR	+ 0.33	+ 0.04		
WAT	+	+		
BAR	-		+	
WAT	+ 0.31		+ 0.32	
WIN	-		-	
AIR	+	+	-	-
WAT	+ 0.22	+ 0.04	+ 0.31	- 0.14
WIN	-	+	-	+
BAR	-		+	-
WIN	- 0.16		- 0.32	+ 0.14
WEA	+		+	-
AIR	+	+		
WAT	+ 0.22	+ 0.04		
WEA	+	+		

AIR	+	+	-	-
WIN	- 0.14	+ 0.04	- 0.31	+ 0.14
WEA	+	+	+	-
BAR		-		
AIR		+ 0.04		
WEA		+		
WAT	+		+	-
WIN	- 0.16		- 0.31	+ 0.13
WEA	+		+	-
BAR	-	-		
WAT	+ 0.29	+ 0.01		
WEA	+	+		
BAR		-	+	-
AIR		+ 0.04	- 0.32	- 0.15
WIN		+	-	+

Fig. 5. Mean abundance per 585 stations of planktivorous (solid bar) and piscivorous (open bar) seabirds in association with wind strength (Beaufort scale)(a) and weather (1= clear to 6= storm) (b) in the South African sector of FIBEX in the Southern Ocean. Statistical significance by ANOVA (BMDP1V).



Discussion

In the Southern Ocean, avian abundance and biomass tend to be high near the Subtropical Convergence (39-43 ^{o} S), Sub-Antarctic and Polar Fronts (47-48^{o}, 51-53 ^{o} S, respectively; Valentine and Lutjeharms, 1983) and the Antarctic Continental Water Boundary (variable), but species richness and abundance do not usually reach levels observed in neritic regions (Griffiths et al., 1982). The overall abundance and non-random distribution of birds in the South African sector of FIBEX was similar to what has been observed generally in the African sector of the Southern Ocean (cf. Griffiths et al., 1982).

In the area considered here, the abundance of planktivores, mostly prions Pachyptila spp. and the blue petrel Halobaena caerulea, is believed to reflect the birds' response to an abundance of plankton and krill which tend to be concentrated near upwelling zones in the latitudes associated with the Antarctic Continental Water Boundary (Marr, 1962; Ainley and Jacobs, 1981; Deacon, 1982).

The co-occurrence of the main concentrations of piscivorous and planktivorous seabirds in areas of relatively warm water (which could be upwelled sub-surface Antarctic water) suggests a dynamic process in the vicinity of 61-63^{o} S which enhanced seabird foraging. I propose that a dynamic process, such as a current-meander induced eddy (Peterson et al., 1982), passed eastwards through the study area and was detected by planktivorous birds as a patch of enriched water containing elevated nutrient or plankton (including euphausids) concentrations. Piscivorous and other seabirds were attracted to the process subsequently, perhaps as larger prey were attracted to the plankton (including

euphausids) concentrations. The concentration of planktivores could have occurred at the start of such a series of hydrological events, followed by the attraction of piscivores as the bird-prey assemblage moved eastwards. I feel that the extreme clumping of birds in certain areas can only represent their attraction to concentrated food resources. The relatively weak association between seabirds and abiotic features indicates a need for more study of the nature of seabird navigation and foraging behaviour. Multidisciplinary input is needed to determine if the redundancy of seabird-abiotic associations (Table 7) reflects the complicated environment, the use by seabirds of multiple cues in locating prey (see Baker, 1978), or, as is most likely, both conditions apply.

The presence of piscivores, chiefly Arctic terns Sterna paradisaea in the south of the survey grid presumably is associated with an enhanced availability of fish at the Antarctic shelf (Targett, 1981) and the presence of ice just south of the grid on which terns can roost. Species in the mixed-diet class, especially the Antarctic petrel Thalassoica antarctica and snow petrel Pagodroma nivea which breed on Antarctica, were also abundant close to the continent, probably because of the ice nearby and increased availability of food at the ice edges and polynas (Zink, 1981; Griffiths, 1983), and at oceanic fronts or other dynamic processes created by the East Wind and Circumpolar currents (Ainley and Jacobs, 1981). The Kerguelen petrel Pterodroma brevirostris predominated amongst the mixed-diet class observed farther north in the vicinity of 61-63°S.

I suspect that planktivores, being relatively small-bodied and requiring frequent meals of small prey items, are more dependent on regular location of patchy sources of abundant food than are

larger species. The distribution of large-bodied seabirds, such as albatrosses, is more random since they apparently require to encounter food items less frequently (Griffiths et al., 1982). All these speculations are in need of further study.

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Appendix 1. Principal food-type and feeding-method groups, body-weights and percentage abundance (numbers of individuals) of species observed in the South African FIBEX sector during February-March, 1981. Diet and feeding-method classification based on data in Ashmole (1971) and unpublished records taken from the FitzPatrik Institute, whih also maintains records of bird weights.

Food-type	Feeding-method	Species	Body-weight (kg)	Abundance (%)
Plankton	Surface-filter	*Pachyptila* spp., prions	0,15	44,50
	Surface-seize	*Halobaena caerulea*, blue petrel	0,20	16,55
	Dip/patter	*Oceanites oceanicus*, Wilson's stormpetrel	0,04	0,38
		Oceanodroma leucohora, Leach's stormpetrel	0,05	0,34
Cephalopods	Surface-seize/scavenge	*Diomedea exulans*, wandering albatross	8,60	0,06
	Surface-seize/scavenge	*Diomedea melanophris*, blackbrowed albatross	3,50	0,02
	Surface-seize/scavenge	*Diomedea cauta*, shy albatross	4,10	<0,01
	Surface-seize/scavenge	*Diomedea chrysostoma*, greyheaded albatross	3,60	0,02
	Surface-seize/scavenge	*Phoebetria fusca*, sooty albatross	2,50	0,05
	Surface-seize/scavenge	*Phoebetria palpebrata*, lightmantled sooty albatross	2,70	0,43
	Surface-seize/scavenge	*Daption capense*, pintado petrel	0,45	0,13
	Surface-seize/scavenge	*Procellaria aequinoctialis*, whitechinned petrel	1,21	1,36
	Surface-seize/scavenge	*Pterodroma lessonii*, whiteheaded petrel	0,75	0,24
	Surface-seize/scavenge	*Fulmarus glacialoides*, Antarctic fulmar	1,00	0,24
Fish	Pursuit-plunge	*Puffinus griseus*, sooty shearwater	0,79	20,50
	Dip/patter	*Sterna paradisaea*, Arctic tern	0,13	9,86
Mixed	Surface-seize/scavenge	*Macronectes giganteus*, southern giant petrel	4,10	0,13
	Surface-seize/scavenge	*Thalassoica antarctica*, Antarctic petrel	0,70	0,80
	Surface-seize/scavenge	*Pagodroma nivea*, snow petrel	0,30	1,23
	Surface-seize/scavenge	*Pterodroma brevirostris*, Kerguelen petrel	0,33	3,37

5.2.2. Gough Island seabirds and hydrography

The distribution of pelagic seabirds in relation to the oceanic habitat of Gough Island

Summary. The distribution and abundance of seabirds capable of flight is described and related to the hydrology of the Gough Island region. Concurrent seabird, hydrographic and hydro-acoustic surveys from the austral spring, 1980, are assessed in order to highlight biotic-abiotic associations. On a macro-scale, the avifauna is explained by Gough Island's position between two major biogeographic zones, and the use of Gough Island as a breeding site by seabirds. On a meso-scale, seabird abundance is greatest in areas of hydrological variability, where the acoustic and net-haul results indicate concentrations of potential seabird prey.

Introduction

Seabird distribution and abundance over the deep-seas is non-random in relation to oceanographic features (e.g. convergences, divergences and fronts) (Pocklington, 1979; Brown, 1980; Griffiths et al., 1982; Section 5.1.1). Close to land, however, seabird distribution is not only influenced by oceanographic features concentrating prey biomass, but also by the location and accessibility of suitable breeding sites (Abrams and Griffiths, 1981; Ainley and Jacobs, 1981; Hunt et al., 1981). In particular, recent studies of meso-scale hydrological processes (<100 km in diameter) have revealed a close association between high relative seabird abundances and short-lived hydrodynamic events (e.g. upwelling), as well as with more permanent features close to the continental margin (e.g. longshore water transport (Joiris, 1978; Ainley and Jacobs, 1981; Hoffman et al., 1981; Schneider, 1983; Section 5.1.2). Similar associations have also been implicated in the vicinity of oceanic islands where offshore prey availability can be strongly influenced by the 'island mass effect' (Ashmole and Ashmole, 1971).

An opportunity arose to study meso-scale seabird-habitat associations far from a continent, near Gough Island during November, 1980. The distribution of seabirds capable of flight was assessed during a detailed hydrological survey of the region (Miller and Tromp, 1982). In addition, hydro-acoustics and mid-water trawling were used to assess the distribution and abundance of potential seabird prey in the form of zooplankton and micro-nekton (Miller, 1982).

Gough Island (40° S, 10°W) is a breeding site for Southern Ocean seabirds, but is also located in the boundary region between the

sub-tropical and sub-Antarctic oceanic zones (Knox, 1960). This paper considers relationships between the pelagic avifauna and hydrodynamic events observed during the above survey as they fit a more global picture of the Gough Island-Tristan da Cunha region derived from satellite-tracked buoys passing through the region during the First GARP Global Experiment (FGGE) (Keeley and Taylor, 1981).

Methods

Observations of seabirds were made by experienced workers aboard the M.V. S.A. Agulhas during October-November, 1980 (austral spring). A hydrological and hydro-acoustic/trawling survey was conducted concurrently aboard the same vessel by the Sea Fisheries Research Institute (Miller, 1982; Miller and Tromp, 1982) around Gough Island (40^{o}S, 10^{o}W, Fig. 1a). Echo-integrator deflections (mm) were used as a relative index of scatterer abundance (Miller, 1982). Seabird counts were recorded in 140 10-minute observations (Anon., 1982), including all birds which flew past, or were passed by, the steaming vessel (mean speed = 23 km h^{-1}). Prevailing current direction and flow rates for the macro-scale region around Gough Island were taken from data made available through the First GARP Global Experiment, (FGGE satellite tracked buoys, Keeley and Taylor, 1981), which was conducted throughout the year preceding this survey.

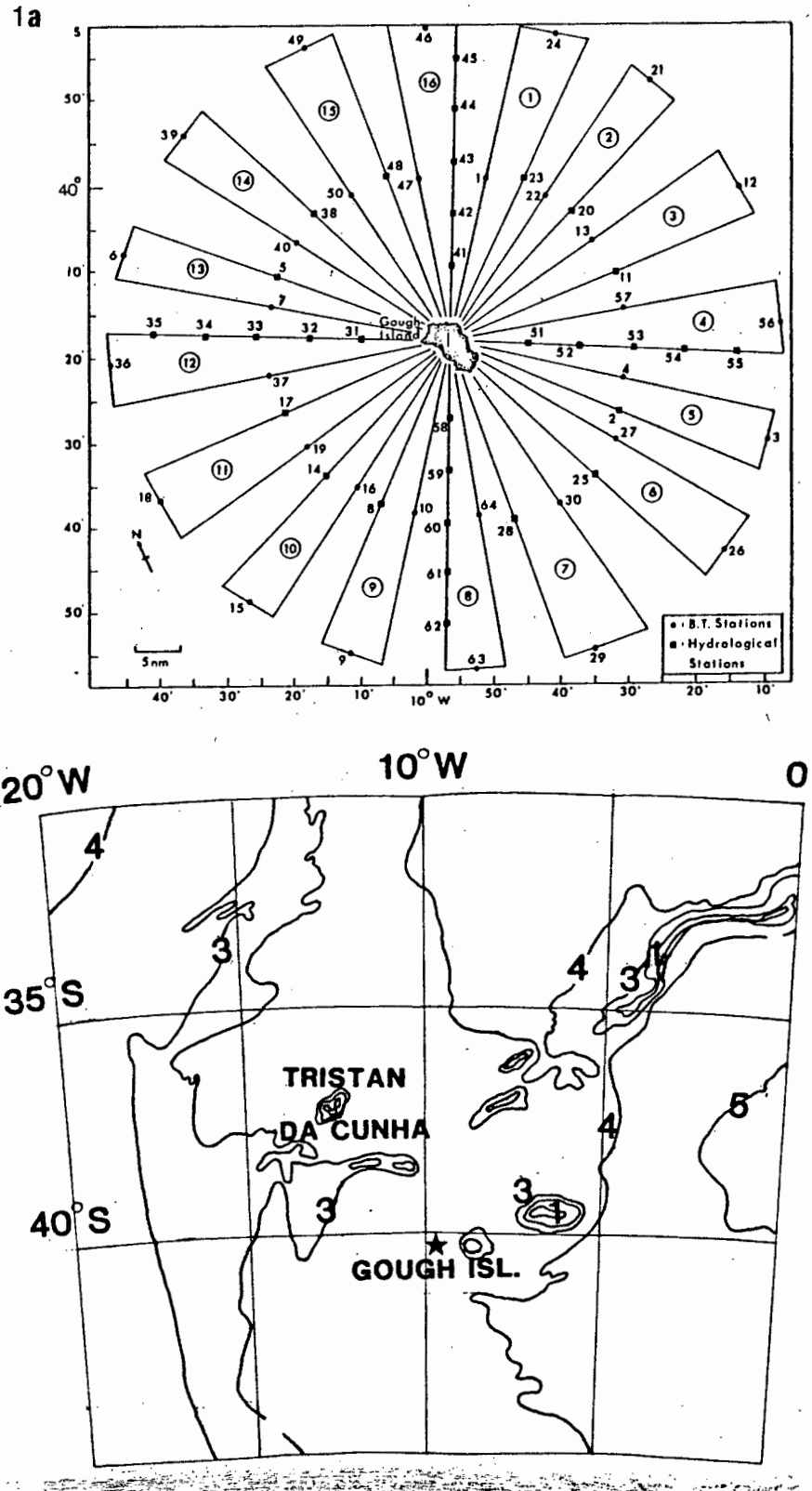
Geography

Gough Island is the most southerly member of the Tristan da Cunha archipelego and constitutes an important feature of the

mid-Atlantic ridge (Fig. 1b). The FGGE buoy composite vector data show that net macro-scale current flow north of Gough Island is easterly (Fig. 1c). South of the Island, the Antarctic Circumpolar Current flows easterly (Deacon, 1982), although the buoy data provides some evidence for transport of surface water northward across 40°S (Fig. 1 c,d). This appears to occur as well as the mixing processes which are inherent in the 'Sub-tropical Frontal' zone (e.g. current meanders, Lutjeharms, 1981; Miller and Tromp, 1982).

Gough Island is the first promontory to break surface and to be encountered by the prevailing easterly currents in the region (Fig. 1). In accordance with current theories, mixing effects would be compounded in the lee of the island (Owen, 1981; Townsend et al., 1983), a fact clearly supported by the FGGE buoy tracks (Fig. 1d). Furthermore, a steep, north-south sea-surface temperature gradient (22-15°C) shown in the buoy data (Fig. 1d) reflects the 'Sub-tropical Frontal' zone (Knox, 1960; Lutjeharms and Valentine, in press) near Gough Island. Data collected during the hydrological survey places the 'Sub-tropical Convergence' slightly to the north of Gough Island, although islands can apparently be characterized by mixed waters of different origin (Miller and Tromp, 1982). More, recently, the 'Sub-tropical Convergence' has been associated with the 14°C surface temperature isotherm and it is postulated that a second 'Sub-Antarctic Front' may be present in association with surface water temperatures of 7-9°C (Lutjeharms and Valentine, in press). In this analysis Gough Island would fall within the 'Sub-tropical Frontal' zone, even though the strongest thermal gradients lie just to the north of the Island.

Fig. 1. The Gough Island-Tristan da Cunha study area showing a) survey grid and hydrographic stations, b) bottom topography (depth in thousands of meters), c) regional mean current vectors from composite FGGE buoy data (courtesy S Patterson, Texas A and M Univ.), and d) current flow taken from individual FGGE bouy tracks near Gough Island (broken lines with numerals (months) represent progression of each bouy in the direction of arrows, SST (^{o}C) in italics).



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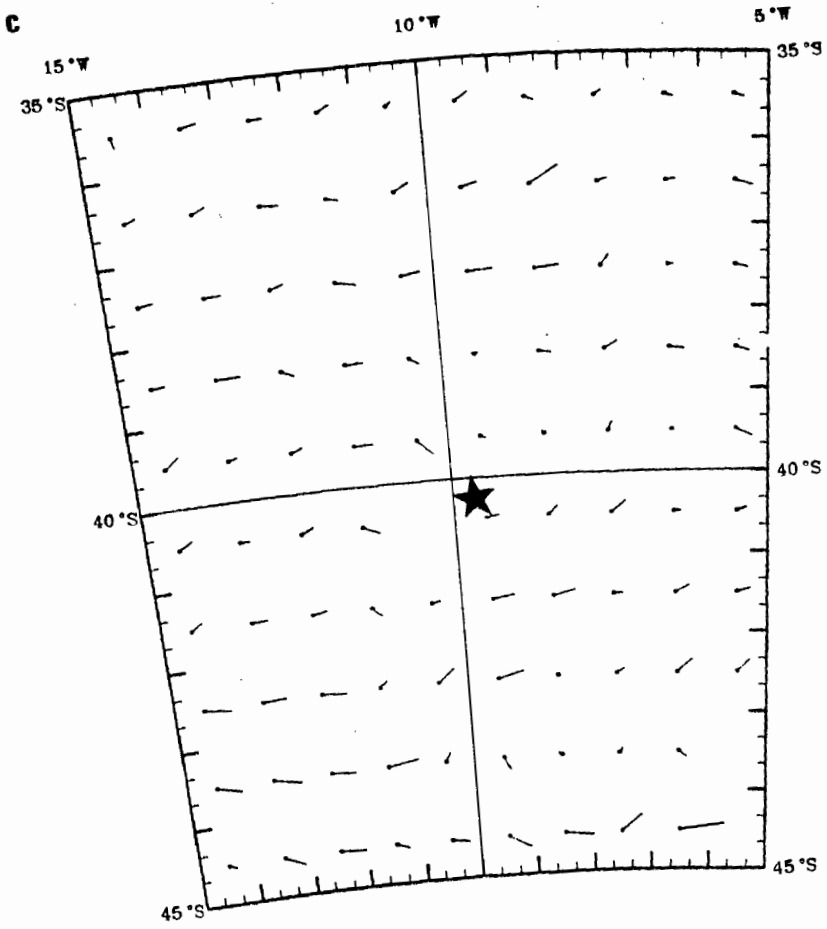

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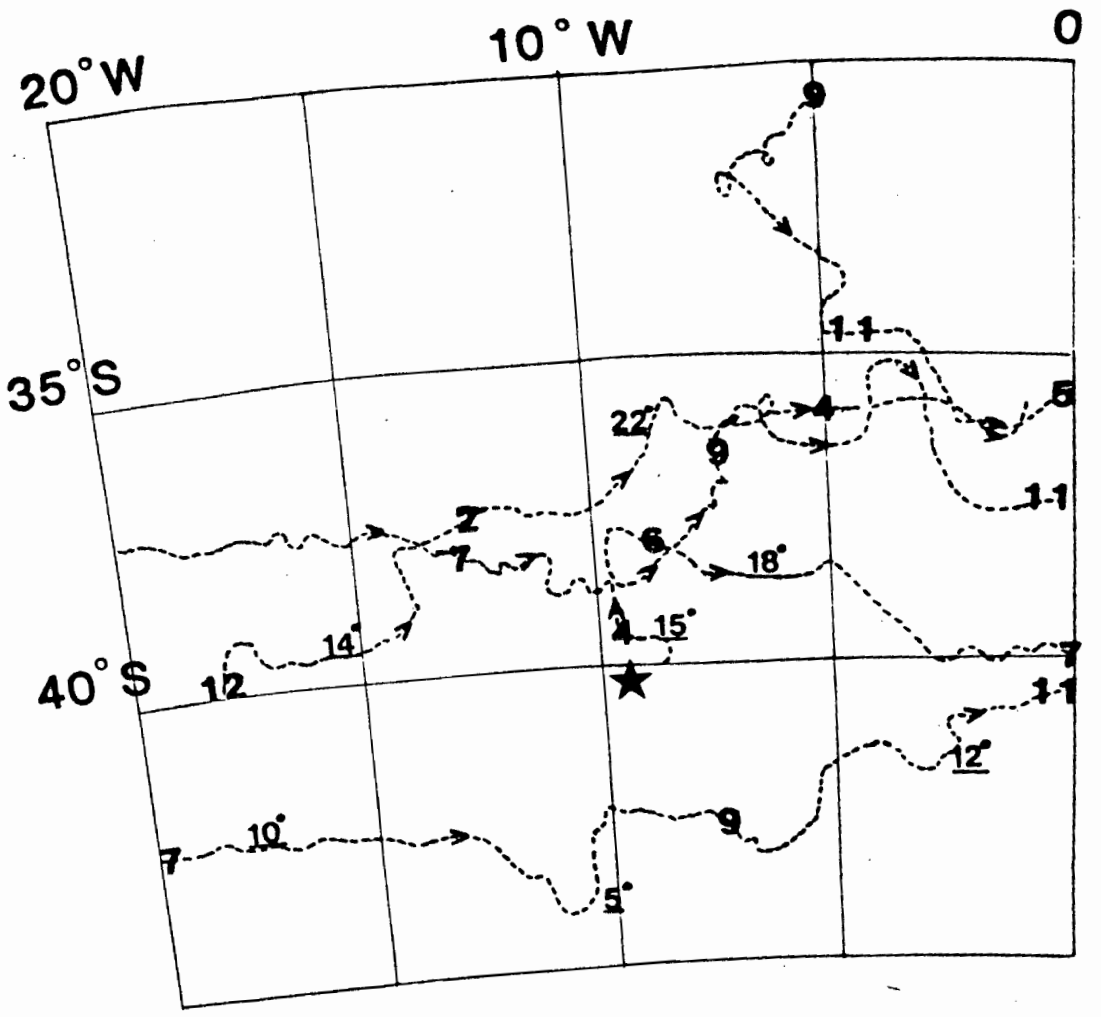


FGGE Drifting Buoys
Mean Velocity
(50 cm/s = —)

Table 1. Correlation coefficients between bird species richness (BSR), species diversity (BSD), abundance (no. of individuals, all species), biomass (live-weight, kg) and abundance by diet-class (see Appendix 1) for avifauna in the vicinity of Gough Island, November, 1980. At the right table margin and along the bottom margin the means (SD) for each variable are given.

Diet-class	BSR	BSD	Abundance	Biomass	Mean	SD
plankton	0.352	-0.315	0.658	0.102	53.2	86.3
squid	0.341	0.096	0.414	0.804	18.3	47.6
fish	0.342	0.179	0.342	0.159	5.0	13.4
mixed	0.426	0.393	0.374	0.388	13.5	27.8
mean	7.7	1.2	90.1	43.8		
SD	2.6	0.5	102.9	51.0		

Seabirds

During the 1980 survey, the pelagic avian community was dominated numerically by plankton-eating species (e.g. prions Pachyptila spp. and diving petrels Pelecanoides spp.), while primarily squid-eating birds accounted for the greatest biomass (e.g. albatrosses Diomedea spp. and large petrels Puffinus gravis, and Pterodroma spp.) (Table 1, Appendix 1). Sub-Antarctic seabird species occurred in abundances typical of the avifauna in latitudes higher than Gough Island (Section 5.1.2) (e.g. Blackbrowed Albatross Diomedea melanophris, Pintado Petrels Daption capense, Whitechinned Petrels Procellaria aequinoctialis, Wilson's Storm Petrels Oceanodroma oceanicus and Kerguelen Petrels Pterodroma brevirostris). Penguins were not considered in this study due to the difficulty of observing them at sea.

Seabird-habitat associations

The distribution of plankton- and squid-eating seabirds (including those breeding on the Island and others) around Gough Island tended to aggregate close inshore and in the lee of the Island (Figs 2 and 3). Seabirds in transit to and from nests probably accounted for a large proportion of the near-island observations. High seabird abundances were apparent in association with the steepest SST gradient of the survey, to the southeast of the Island, and with a tongue of relatively warm surface water (>12^{o}C) to the north of the Island (Figs 2 and 3).

Vertical temperature profiles and salinity data indicate a sub-surface advection of cold water (minimum 9^{o}C) to the east of the Island which coincided with a similar vertical advection of

Fig. 2. The distribution of plankton-eating seabirds (individuals per station, approx. 4 km^2) for Gough Island survey (area within dashed lines). Sea-surface temperature (^{o}C) from Miller and Tromp (1982)

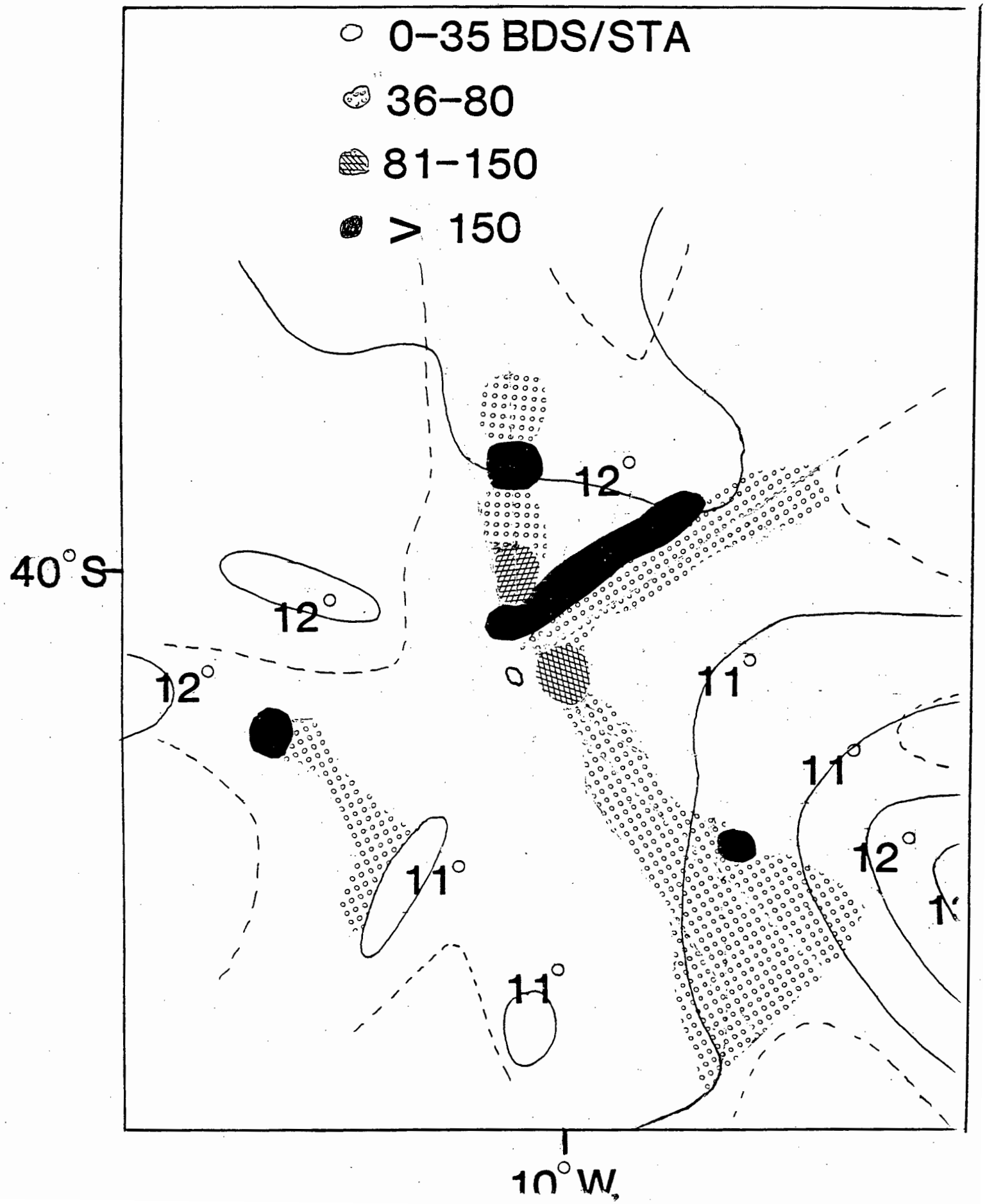
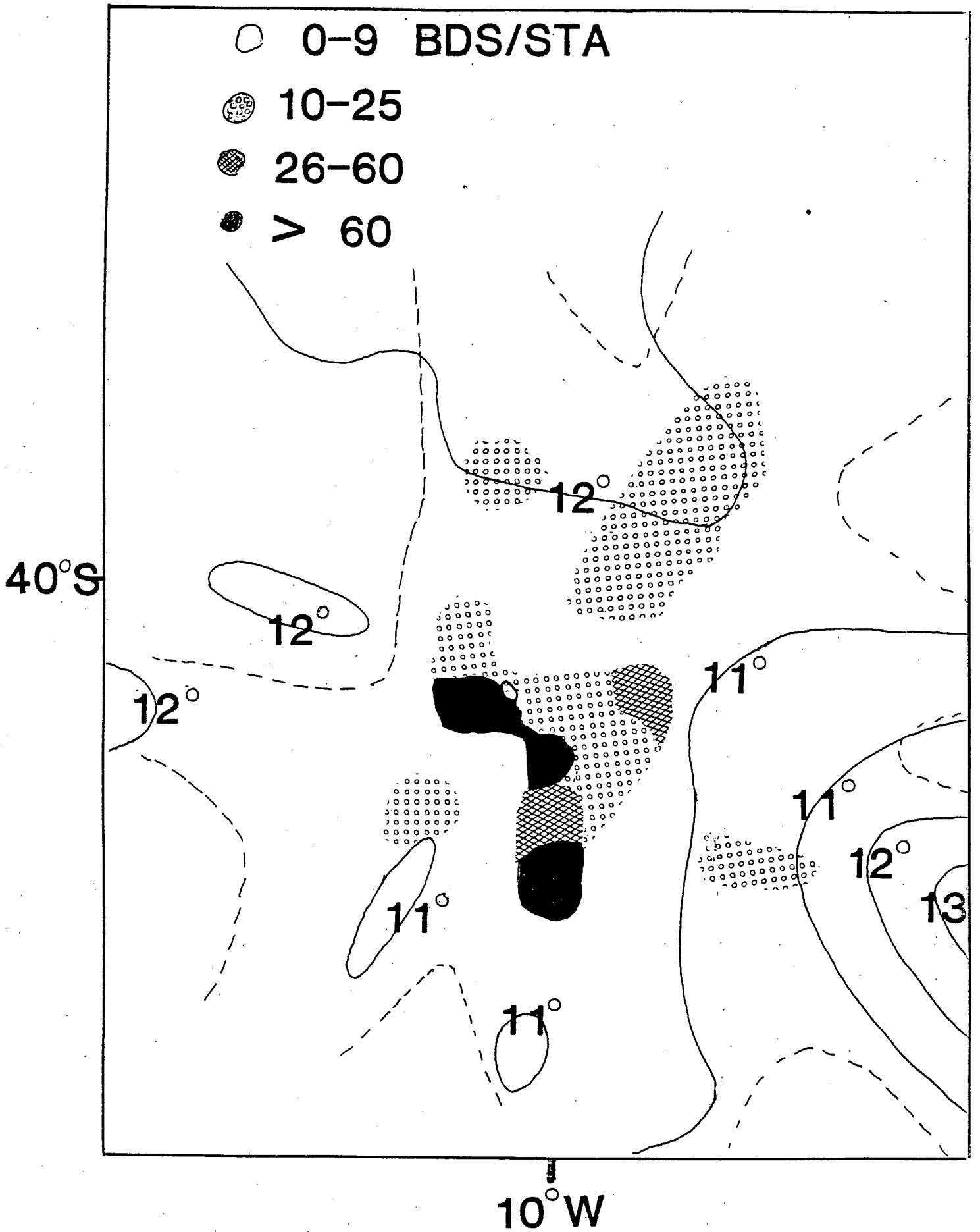


Fig. 3. The distribution of squid-eating seabirds (individuals per station, 4 km^2) for Gough Island survey (area within dashed lines). Sea-surface temperature (^{o}C) from Miller and Tromp (1982)



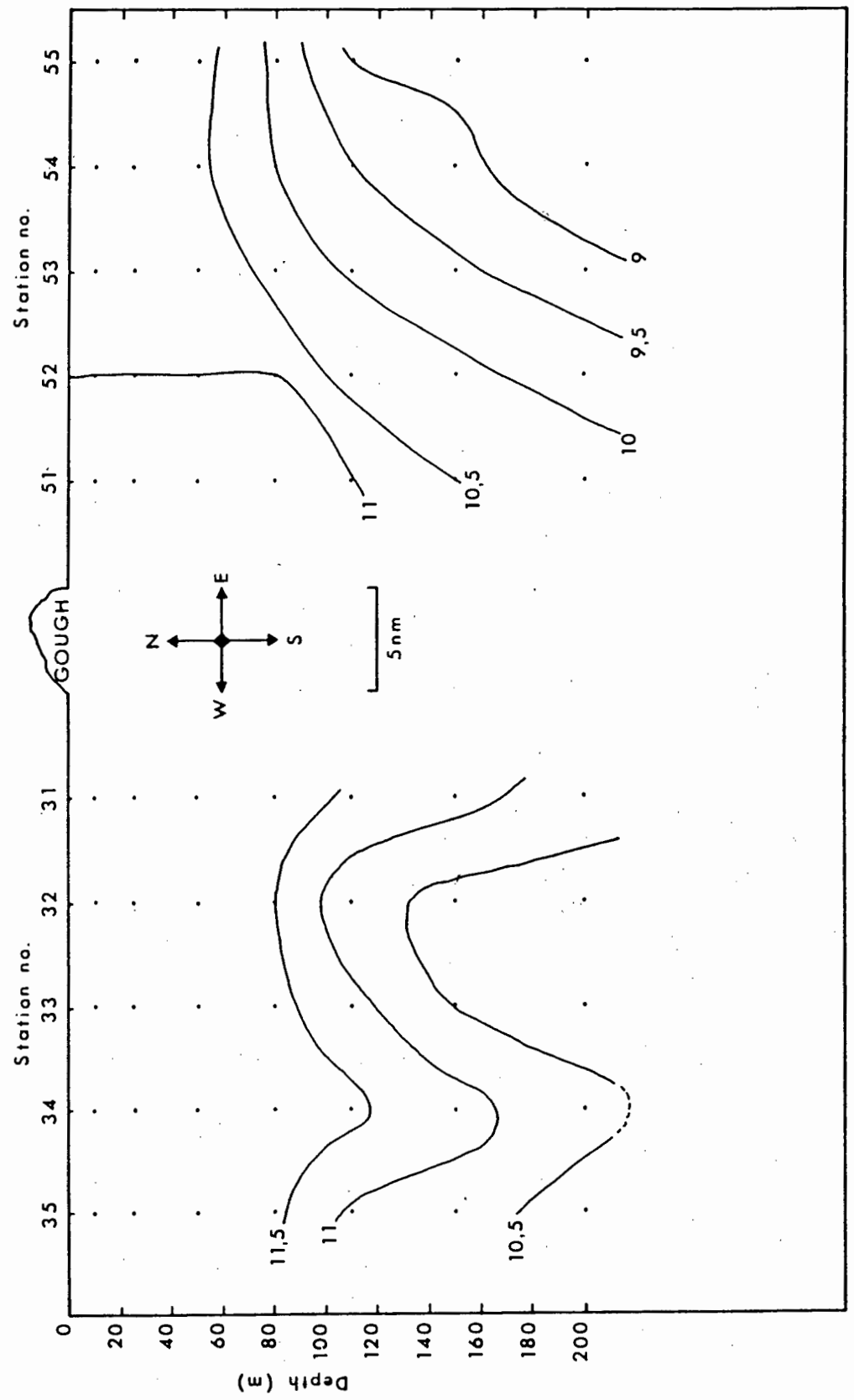


Fig. 4. Vertical temperature (^{O}C) profile on west-east survey leg, in the vicinity of Gough Island, after Miller and Tromp (1982)

nutrient salts (Fig. 4, Miller and Tromp, 1982). To the south-east of Gough Island, plankton-eating seabirds were abundant over the cool water on the western edge of the SST gradient (Fig. 2). Squid-eating birds co-occurred partially with planktivores but were most abundant in cooler waters (<11^{o}C) close inshore and in the cool water on the western edge of the SST gradient south-east of the Island (Fig. 3). Acoustic and net-haul results suggest a concentration of zooplankton in the lee of the Island (Fig. 6) (Miller, 1982), particularly close to the strong SST gradient (Figs 4 and 5b). It seems likely, therefore, that foraging birds were responding to the effects of nutrient enhancement and increased zooplankton abundance in the lee of the Island.

Surface nitrate exhibited a strong distributional gradient directly east of the Island, extending north to south (Fig. 5b). A relatively steep phosphate gradient coincided with the nitrate feature to the east of the Island, but to the north-east turned to the west (Fig. 5a, b). High abundance of plankton-eating birds were encountered from close inshore through the position where the nitrate-phosphate gradients crossed and within the 12^{o} C surface-isotherm (Figs 2 and 3). Squid-eating birds overlapped with planktivores, and were abundant across the nitrate-phosphate interface, in both the cool and warm water (Fig. 3).

Miller and Tromp (1982) propose that the sub-surface temperature maximum north of the island indicated a sub-surface intrusion of sub-tropical water (Fig. 7). Here, plankton-eating seabirds increased gradually up to, and decreased away from, the 12^{o}C isotherm (Fig. 2), which coincided with the east-west surface phosphate gradient (Fig. 5). Squid-eating birds again co-occurred

Fig. 5. Horizontal profiles (gμ-at/l) of sea-surface phosphate (a) and nitrate (b), in the vicinity of Gough Island, after Miller and Tromp (1982)

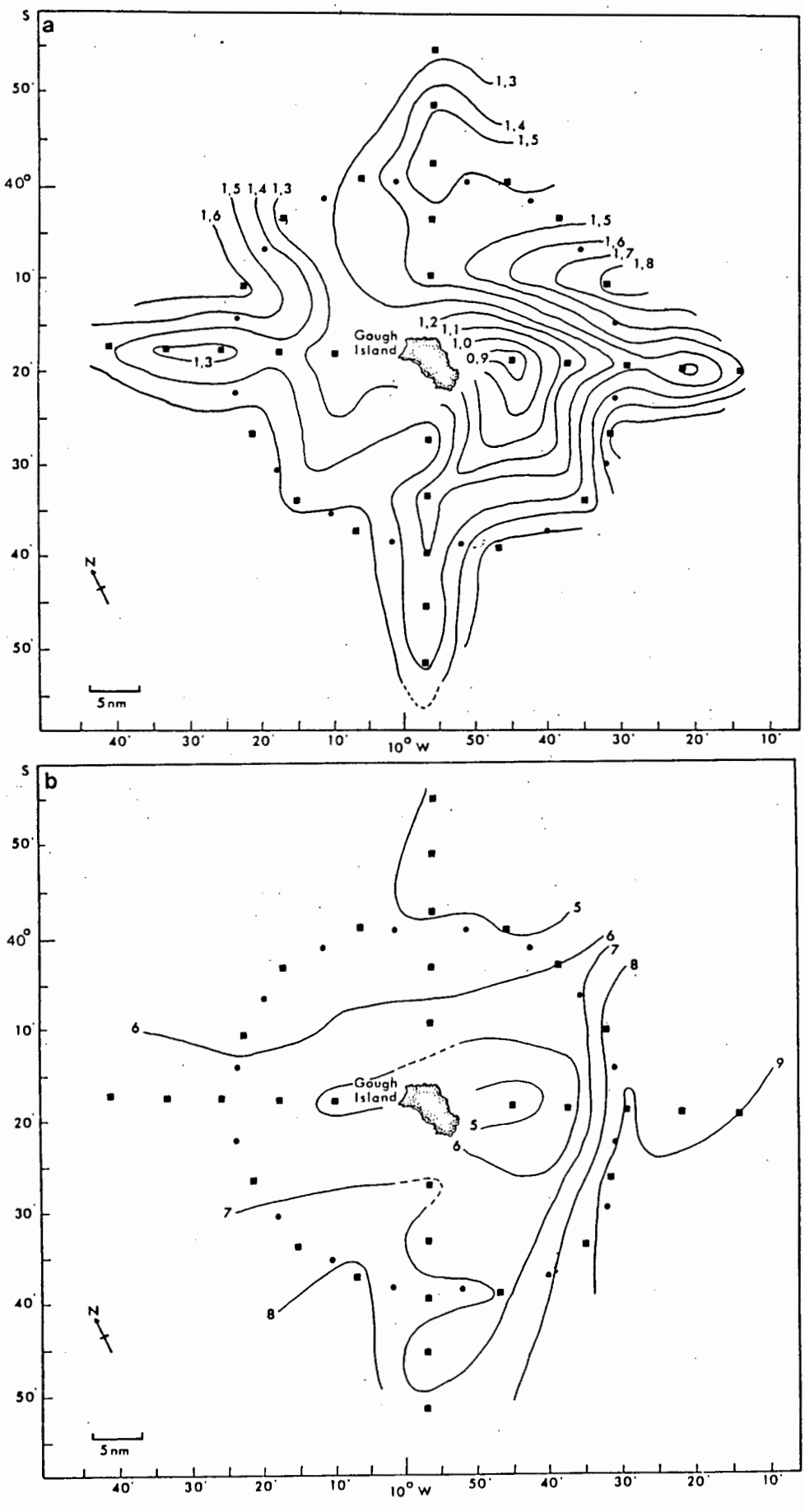


Fig. 6. The distribution of echo-integrator deflections (mm) in the vicinity of Gough Island, after Miller (1982)

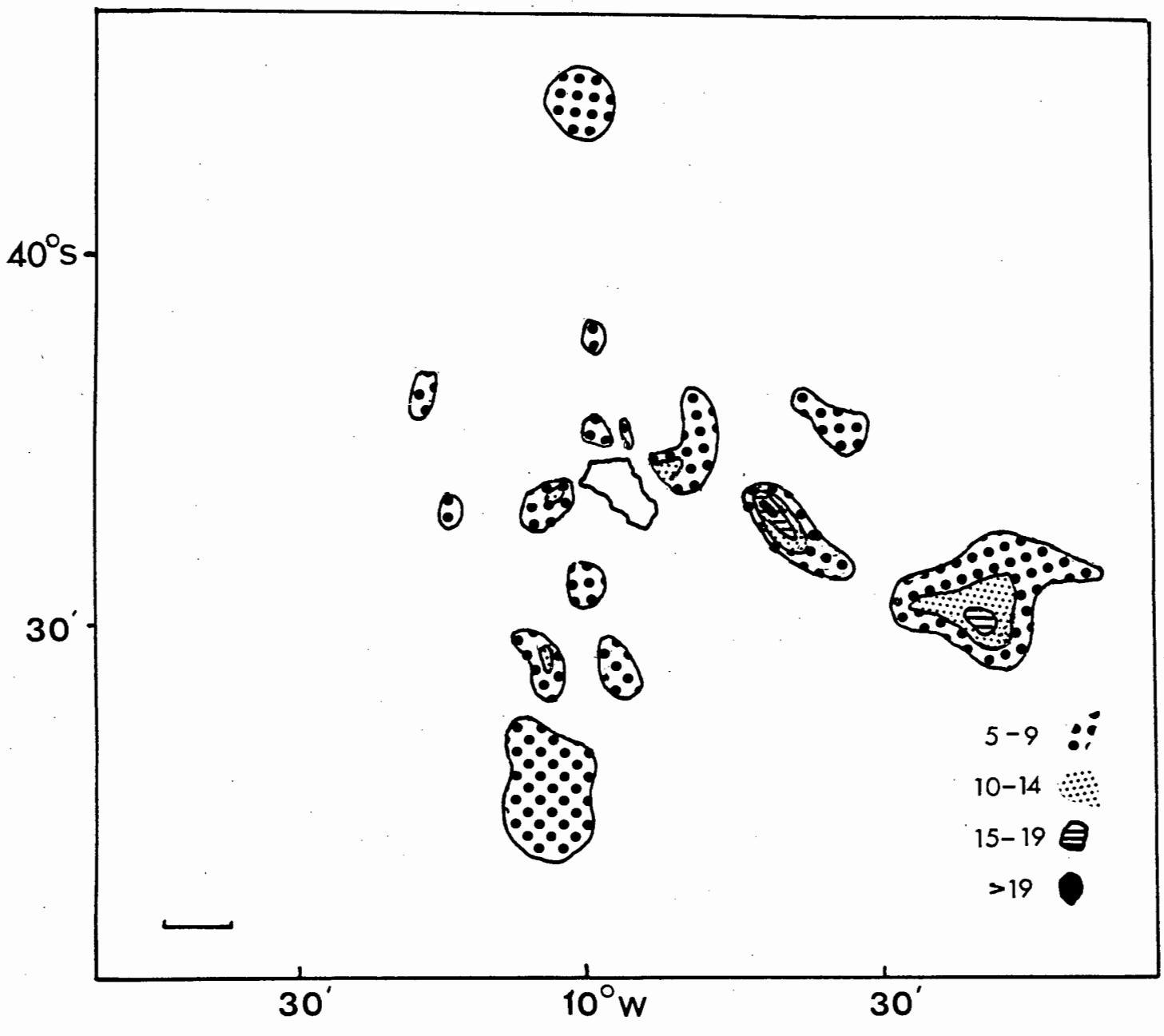
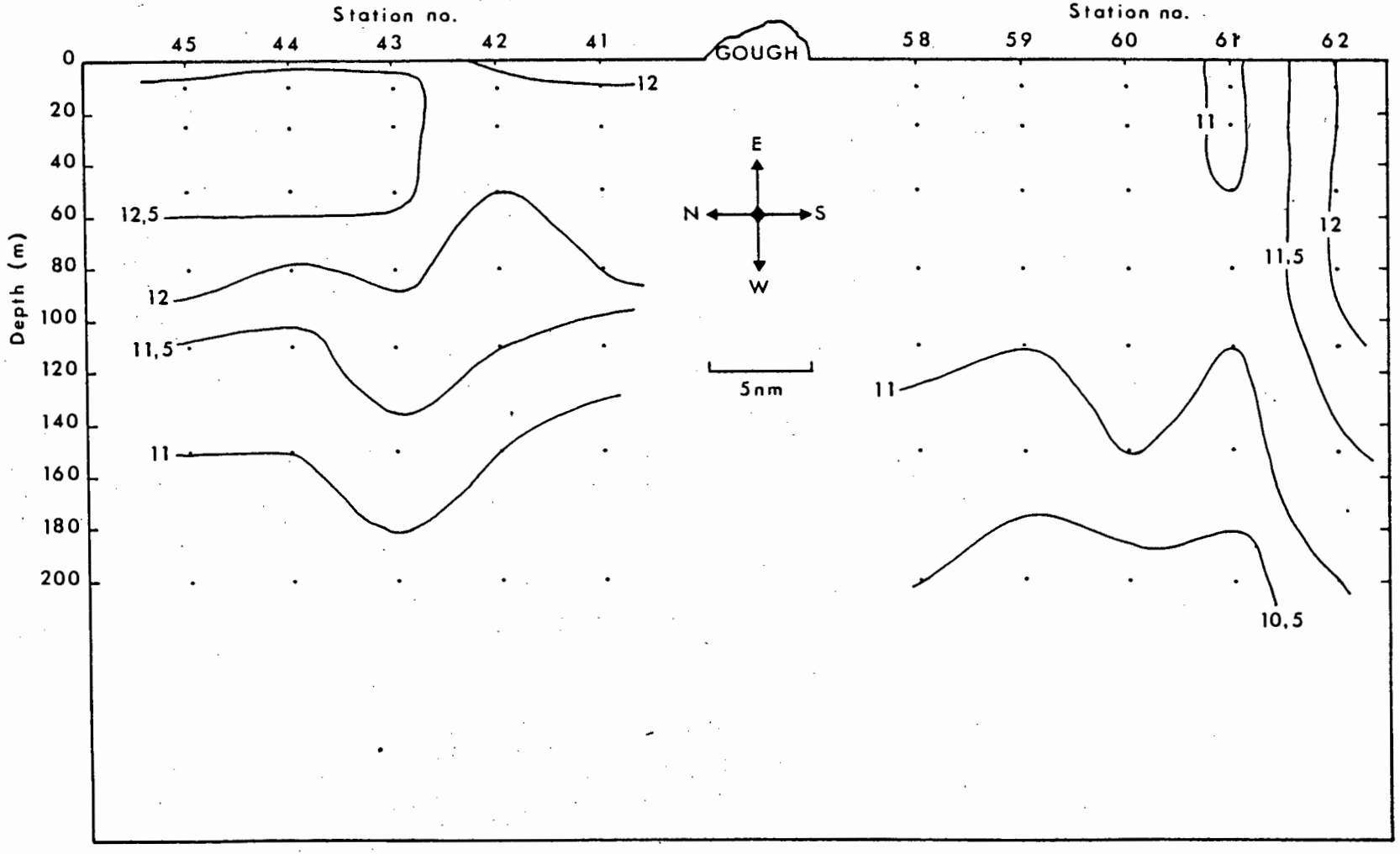


Fig. 7. Vertical temperature (^{o}C) profile on north-south survey leg, in the vicinity of Gough Island, after Miller and Tromp (1982)



with planktivores but were most abundant over cooler waters (<11° C) close inshore and near the south-eastern edge of the warm-water tongue (Fig. 3).

Enhanced acoustic backscatter was recorded where planktivorous seabird density was greatest on the north-south survey leg and south-east of the Island (Figs 2 and 6). Seabird abundance to the south-west of the island was high in association with both a patch of cold water and enhanced acoustic scatter (Figs 2,3 and 6) (Miller, 1982).

Discussion

Seabird abundances observed during November, 1980, in the vicinity of Gough Island were substantially greater than those in the Sub-tropical Frontal zone or in the vicinity of the Antarctic Polar Front of the African sector of the Southern Ocean; both areas of high aerial seabird density (Griffiths et al., 1982; Section 5.1.1). The pelagic avifauna in the vicinity of Gough Island during November, 1980, included sub-tropical and sub-Antarctic species (Section 5.1.1), and was a mixture of non-breeding species and species which breed on the Island (Watson, 1975). Several of the species observed during the survey breed at localities some distance from the Island and were present in sufficiently high abundance (Appendix 1) (Section 5.1.1) to suggest a possible attraction to the area as a foraging ground. The Blackbrowed Albatross breeds at South Georgia (54° S; 78° W) (Watson, 1975) and migrates through the Gough-Tristan area on its way to its austral winter foraging grounds off the South African/Namibian coasts (Morant et al., 1983). As a result, birds undertaking such migrations may stop at, or linger in transit, in the vicinity of Gough Island to feed and possibly rest.

The marine productivity in the waters close to Gough is probably enhanced in two ways. First, as the island constitutes a breeding site for the large numbers of birds, the relatively narrow neritic zone is probably enriched by nutrient salt run-off resulting from ephemeral leaching of guano deposits into near-shore water (Selickman and Golovkin, 1972; Burger et al., 1978; Frost, 1979; Miller and Tromp, 1982). The shallow waters close to the Island support extensive faunal and floral diversity and have been shown to be especially rich in macrophytic algae (Womersley, 1954; Knox, 1960; Chamberlain, 1965; Koop and Anderson, 1982), ichthyofauna (Penrith, 1967) and the crustacean, Jasus lalandii (Heydorn, 1969). The present survey was undertaken in early summer when bird incubation shifts are still sufficiently long to allow parent birds to forage far from the Island. For this reason, relatively high abundances of birds close inshore probably not only indicates breeding activity but also that considerable food is available near the Island. Secondly, since the shelf is narrow (Fig. 1b), like so many oceanic islands, waters around Gough Island probably exhibit many of the characteristics associated with deep-sea frontal zones and their mixing processes (Van Dorn et al., 1967; Owen, 1981; Townsend et al., 1983). Under such circumstances, it is postulated that vertical and horizontal oceanic mixing would enhance productivity in the deeper waters surrounding the Island and especially in its lee (Miller and Tromp, 1982).

As a result of the relatively high salinity encountered, Miller and Tromp (1982) suggest that waters in the lee of the Island may be susceptible to the effects of downstream baroclinic eddy formation, which, in combination with both horizontal and vertical mixing, could account for the co-occurrence of temperate and

saline water. Combined with effects of both horizontal and vertical mixing induced by topographical effects (e.g. eddy formation) and possibly upwelling, it would appear that biological productivity in the area in the lee of Gough Island is probably affected by relatively small-scale hydrodynamic events.

Squid- and plankton-eating birds co-occurred in their greatest abundances at and near the warm water to the north of the Island and in the temperature/nutrient 'fronts' north-east and south-east of the Island. Hunt et al. (1981) describe how oceanic temperature fronts, acting as barriers to plankton movement, influenced seabird dispersion in the Bering Sea. Such 'barriers', if broken by horizontal transport due to a frontal meander (with eddies or rings being shed), may produce patches of enhanced prey diversity (Wiebe et al., 1976).

As already stressed, Gough Island lies at the northern boundary of the Antarctic Circumpolar Current and thus provides a unique biotope for Southern Ocean seabirds by virtue of its position. The persistence of oceanic mixing processes due to the topographical effects of the Island could sustain the relatively steep environmental gradients. As such, the area would be analagous to a biogeographical boundary zone which would tend to concentrate and support a diverse aquatic fauna (see Owen, 1981 for review). Joiris (1978; 1983) has shown that restriction of plankton distribution by hydrodynamic variability directly affects seabird distribution in the North Sea. However, the relationships between seabird distribution and the Gough Island oceanic 'fronts' cannot be confirmed as causative, since associations between bird abundance and habitat structure represent second-order bird-prey correlations (Section 5.1.2).

Unfortunately the small sea-surface temperature gradients (i.e. 11-13 ^{o}C) prevailing at the time of the survey do not provide unequivocal evidence for frontal discontinuities in the absence of small-scale measurements of current flow (e.g. see Hofmann et al., 1981). Both the Hunt et al. and Joiris projects were in high latitudes where relatively small gradients of sea-surface temperature were signatures of fronts (i.e. < 4^{o}C, Joiris, 1983; Kinder et al., 1983). If warm water distribution during this study was indicative of frontal expressions, then it could have provided conditions for enhanced plankton production and in turn a rich foraging ground for seabirds. Accordingly, nutrients or prey normally unavailable to squid and fish would occur in a confined area where the concentration of several trophic levels could attract seabirds.

At present, interpretation of seabird-habitat associations lacks sufficient input on the effect of weather on bird activity and behaviour. Mendelsohn (1981) has shown that prions (Pachyptilla spp.) avoid inclement weather conditions around the Prince Edward Islands (southern Indian Ocean). Conversely, Section 5.1.2 showed little correlation between seabird abundance and selected meteorological parameters. It is conservative to conclude that near Gough Island, observations of low bird density may have been linked with harsh weather. However, no large portions of the bird survey were missed due to harsh weather.

Further study of the Gough Island area is indicated, with collection of detailed hydrological and meteorological data concurrently with biological and avifaunal surveys. Such research must also determine, through a time series approach, if the non-breeding birds around Gough Island are present as short-term

transients or because the area consistently offers easy access to a diverse prey community.

Conclusion

Seabirds exhibited non-random distribution over waters close to Gough Island. Hydrological and hydro-acoustic data suggest the possible attraction of seabirds to areas characterized by hydrological variability. Distribution patterns observed during the survey suggest a co-occurrence between seabirds feeding relatively far offshore and regions of hydrodynamic discontinuity, and between seabirds feeding close inshore and the neritic zone.

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Appendix 1. Principal food-type classes, body mass (live weight), percentage abundance (numbers of individuals) and breeding status at Gough Island (B = breeder, M = non-breeder) of species observed in the vicinity of Gough Island, November, 1980. Food-type classes based on Ashmole (1971) and unpublished records taken from the FitzPatrick Institute which also maintains records of bird weights and breeding status

Food-type		Breeding status	Mass (kg)	%
Plankton				
Pachyptila spp.	prions	B	0.15	56.62
Oceanites oceanicus	Wilson's Stormpetrel	M	0.04	0.41
Fregatta tropica	Blackbellied Stormpetrel	M	0.06	0.01
Fregatta grallaria	Whitebellied Stormpetrel	B	0.05	0.13
Pelecanoides spp.	diving petrels	B	0.12	1.51
Phalaropus fulicarus	Grey Phalarope	M	0.03	0.02
Garrodia nereis	Greyrumped Stormpetrel	B	0.05	0.17

Squid

Diomedea exulans	Wandering Albatross	B	8.60	1.32
Diomedia melanophris	Blackbrowed Albatross	M	3.50	0.95
Diomedia chrysostoma	Greyheaded Albatross	M	3.60	0.02
Diomedea chlororhynchos	Yellownosed Albatross	B	2.00	0.69
Phoebetria fusca	Sooty Albatross	B	2.50	2.36
Fulmarus glacialoides	Antarctic Fulmar	M	1.00	0.02
Daption capensis	Pintado Petrel	M	0.45	1.55
Pterodroma macroptera	Greatwinged Petrel	B	0.58	0.07
Pterodroma incerta	Atlantic Petrel	B	0.52	1.66
Procellaria aeguinoctialis	Whitechinned Petrel	M	1.21	0.43
Procellaria cinerea	Grey Petrel	M	1.03	0.02
Puffinus gravis	Great Shearwater	B	0.95	11.97

Fish

Puffinus griseus	Sooty Shearwater	M	0.79	0.29
Puffinus assimilis	Little Shearwater	B	0.23	5.26
Sterna vittata	Antarctic Tern	B	0.14	0.04

Mixed

Macronectes giganteus	Southern Giant Petrel	B	4.10	0.29
Macronectes halli	Northern Giant Petrel		5.20	0.21
Pterodroma brevirostris	Kerguelen Petrel		0.33	6.39
Pterodroma mollis	Softplumaged Petrel	B	0.31	7.83
Stercorarius spp.	Skua	M	0.50	0.25

5.2.3. FIBEX hydrography and krill distribution

Relationships between seabirds, krill and hydrography in the South African area of FIBEX

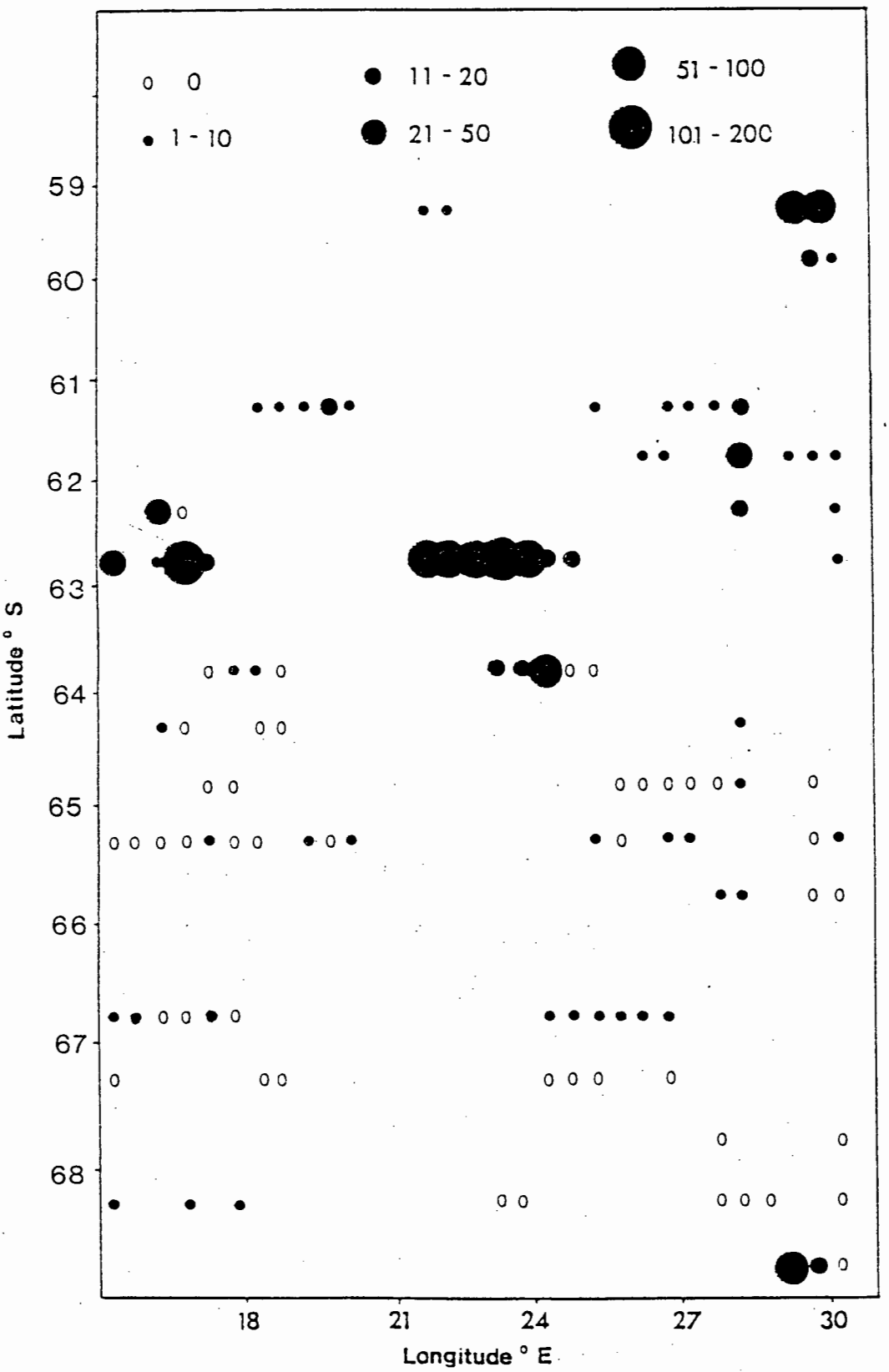
Introduction

The First International BIOMASS Experiment (FIBEX) aimed at assessing the distribution and abundance of krill Euphausia superba and some of its predators in the Southern Ocean (Anon., 1981). Here, I relate aerial seabird distribution (excluding penguins, because they are difficult to detect and count at sea) to krill distribution in the South African area of FIBEX during February-March, 1981 (Fig. 1). These relationships are compared with the distribution of seabirds in the same area during March-April, 1980, and with hydrographic information for the same area.

Methods

The distribution of seabirds in the South African FIBEX area (between 60^{o}S and 69^{o}S, and 14^{o}E and 31^{o}E) was assessed using the BIOMASS Seabird Mapping Scheme (Anon., 1982) during February-March, 1981 (Section 5.2.1) and during March-April, 1980. Concurrent with the seabird observations during 1981, the distribution of krill (g m^{2}) was determined from 30-, and 120-minute interval readings of a hull-mounted echo-sounder (Hampton, 1985). Seabird distributions observed during March-April, 1980, as well as those reported for the South African area of FIBEX (Feb.-March, 1981), are related to a recently described hydrological feature of the region (Gordon and Huber, in press; A.L. Gordon, pers. comm.). Seabird distribution is analysed as in Section 5.2.1, in terms of abundances of species lumped by principal diet: plankton (PF), squid (CF), fish (FF) and mixed-diet (MF). The composite of sea-surface temperature for February-March, 1981, is from data logged with seabird counts and those logged by CTD casts of the Sea Fisheries Research Institute.

Fig. 1. The distribution and abundance (no. individuals) of seabirds (all species) in the South African FIBEX area, February-March, 1981 (after Section 5.2.1).



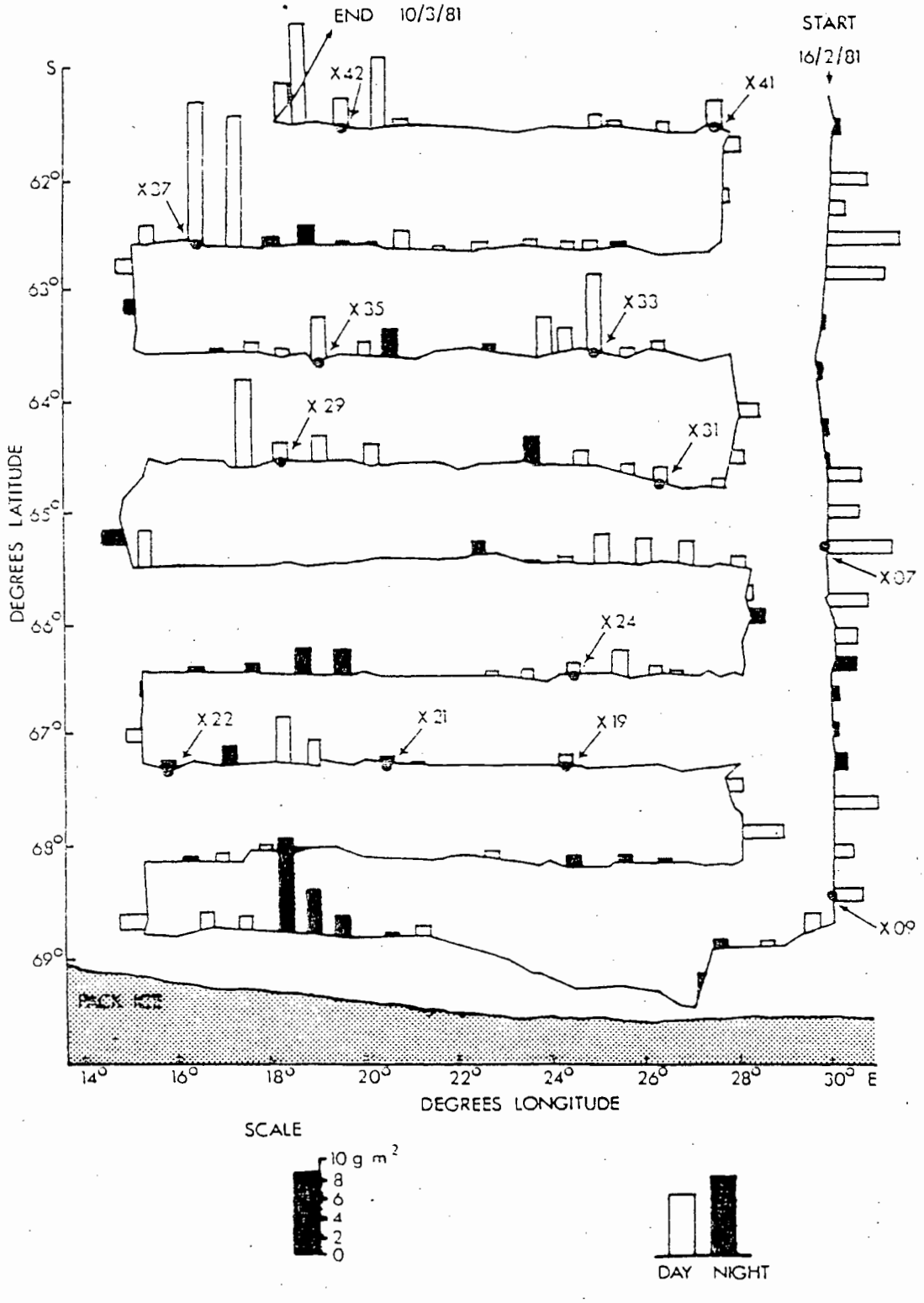
Results and discussion

Planktivores and piscivores were the most abundant seabirds in 1981, and were concentrated in a narrow latitudinal band between 61°S and 63°S (Fig. 1). Krill were generally patchy throughout the survey area. Acoustic evidence (echo-integrator deflections (mm)) for the highest sub-surface (i.e. > 10 m depth) densities (g m^{-2}) (Fig. 2) was obtained in the same latitudinal band as the highest seabird abundance (Fig. 1), and coincident with a patch of seabirds between 63°and 64°S. In the northern half of the survey area, where predators and putative prey were most abundant, the variance in bird abundance and krill density both differed significantly by one degree of latitude (Table 1), which was the finest resolution of the data available for analysis. Consequently, correlations of high-density planktivore patches with high relative abundance of krill were not well represented in regression models. Increases in seabird abundance occurred in the vicinity of high krill abundance (according to 30-minute interval records) along the transect of highest bird abundance (Fig. 3).

Table 1. Analysis of variance (d.f. 3,158) of seabird abundance (no. individuals per 10-min) and krill density (g m^{-2}) by one degree latitudinal bands between 61°S and 65°S during March, 1981. Krill variables are the 30- and 120-min echo-integrator interval density estimates (g m^{-2})

	Seabird abundance			Krill	
	Planktivores	Piscivores	All species	(30-min)	(120-min)
F-value	6.97	5.04	8.84	4.15	8.55
Probability	0.001	0.002	0.001	0.007	0.001

Fig. 2. Continuous time sequence of krill density (g m^2) based on 30-min echo-integrator readings throughout the survey of February-March, 1981, in the South African FIBEX area (after Hampton (1985)).



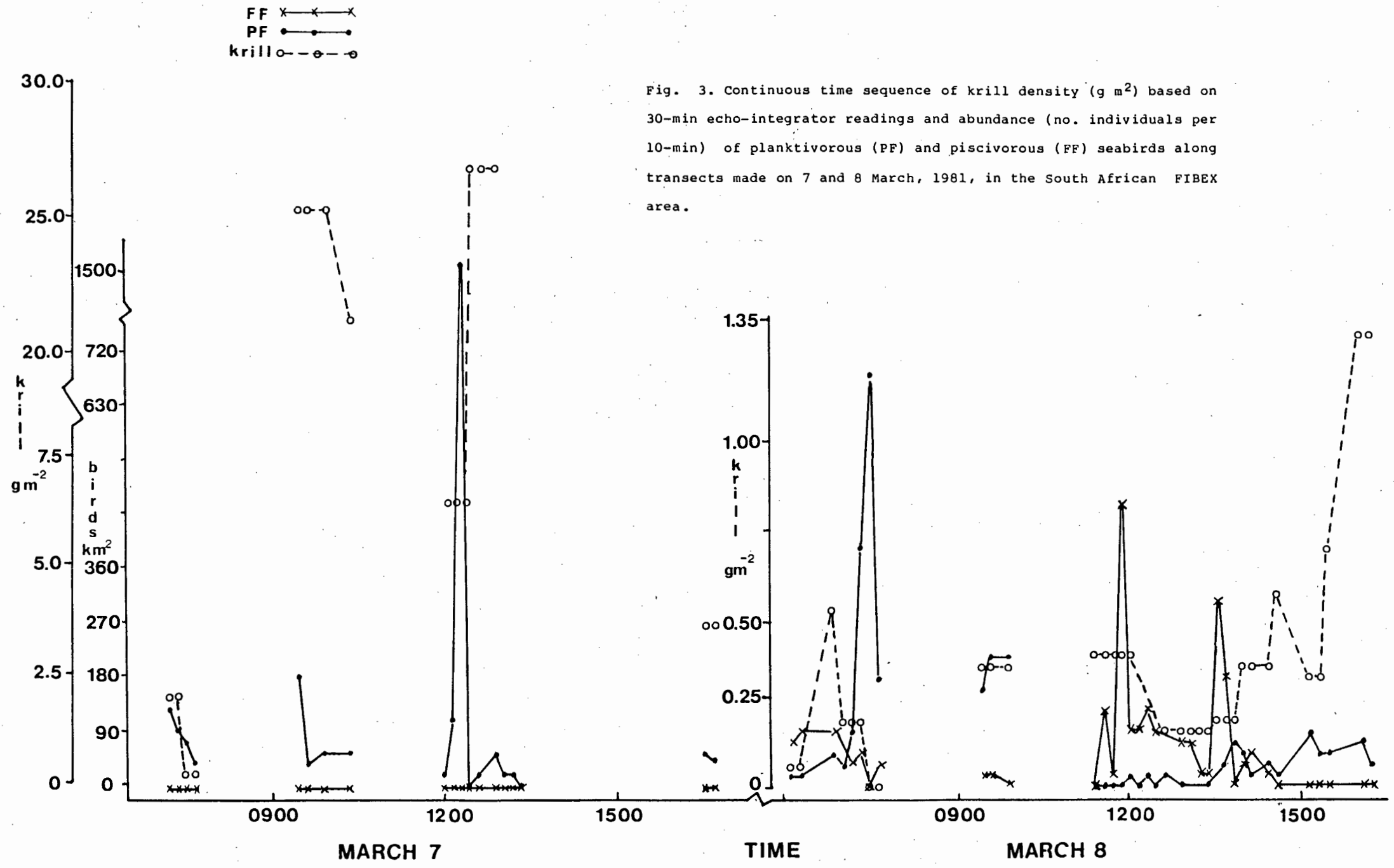


Fig. 3. Continuous time sequence of krill density (g m^2) based on 30-min echo-integrator readings and abundance (no. individuals per 10-min) of planktivorous (PF) and piscivorous (FF) seabirds along transects made on 7 and 8 March, 1981, in the South African FIBEX area.

In both years (March-April, 1980 and February-March, 1981) planktivores featured prominently between 61°and 64°S (Figs 1 and 4). In 1981, some of the concentrations of krill and seabirds coincided with patches of relatively warm sea-surface temperature (Figs 2, 4 and 5). A preliminary assessment (Section 5.2.1) suggested that a meso-scale hydrodynamic feature (i.e. an eddy) passed eastwards through the study area during February-March, 1981, as a patch of prey-rich water. This could explain the patchy occurrence of planktivores along the western part of the transects of 7-8 March, and the patchy occurrence of piscivores along tne eastern part of these transects (Fig. 3).

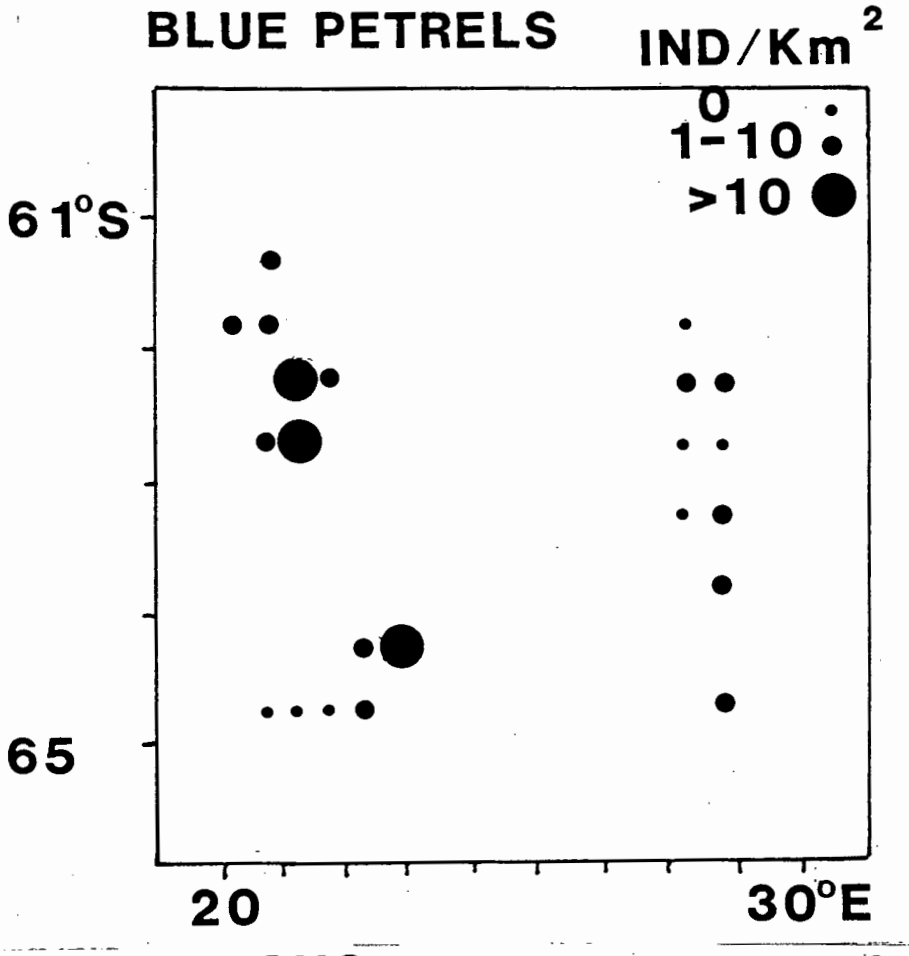
The existence of a front between the return flow of the eastern Weddell Gyre and an anti-cyclonic gyre passing through the South African FIBEX area has been postulated (Gordon and Huber in press). This inter-gyral front appears to originate near the Maud Rise (65°S, 0), and runs north-east. It may have been present across the north-west corner of the South African FIBEX survey area during 1981 (Fig. 5). Warm-core eddies are shed to the west of the inter-gyral front into cold Weddell Gyre waters (Gordon and Huber, in press). If, during February-March, 1981, cold-core eddies were shed from the inter-gyral front eastwards, into the South African FIBEX area, they could have caused the heterogeneity observed in the sea-surface temperatures during the survey (Fig. 5). However, the main direction of flow in the north-west corner of the South African FIBEX area is south-westerly, so that my proposal (Section 5.2.1) of an easterly movement in sea-surface features seems an over-simplification.

Processes associated with the inter-gyral front might enhance the availability of krill to seabirds. The features studied by Gordon

and Huber (in press) are not expressed at the sea-surface, but the pycnocline is within 50 m of the surface at the north-eastern end of the inter-gyral front, in the vicinity of the high seabird abundances found during two successive summers. Eddies shed eastwards from the front would not recross the front (A.L. Gordon, pers. comm.), and could contain plankton and nekton (including krill) of Weddell Sea origin. Such eddies would not provide strong sea-surface expressions, but even small SST and salinity fluxes in Antarctic waters might enhance biological production (Tranter, 1982; Ronner et al., 1983). Conditions are conducive to biological enhancement where a pycnocline nears the surface (A.L. Gordon, pers. comm.), because nutrients would be readily available to surface mixing processes and light, thereby enhancing a change from a purely deep-sea, oligotrophic habitat to a habitat containing meso-scale 'parcels' of eutrophic water which could support seabird prey. Such events do occur in Antarctic waters (Tranter, 1982).

I suggest that the occurrence of relatively warm water, krill and seabirds (in two years) in the vicinity of the position proposed for the inter-gyral front was the result of hydro-dynamic processes which mixed nutrients from the shallow pycnocline of the inter-gyral front, and brought together, near the sea-surface, phytoplankton, zooplankton and krill in numbers large enough to attract seabirds. Further surveys of the area should aim to test the relationship between the fauna and the oceanic dynamics, and attempt to resolve the nature of hydrological events to the east of the inter-gyral front.

Fig. 4. The distribution and abundance (no. individuals km^2) of planktivorous birds (Halobeana caerulea, and Pachyptila spp.) in the South African FIBEX area during March-April, 1980.



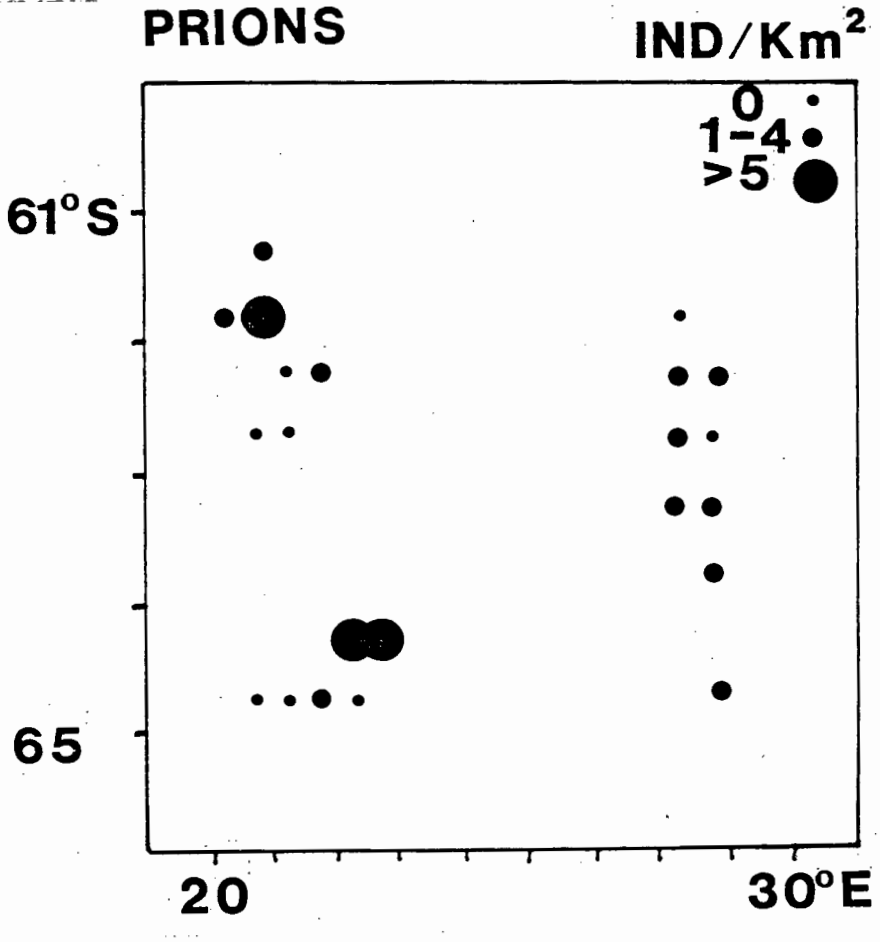
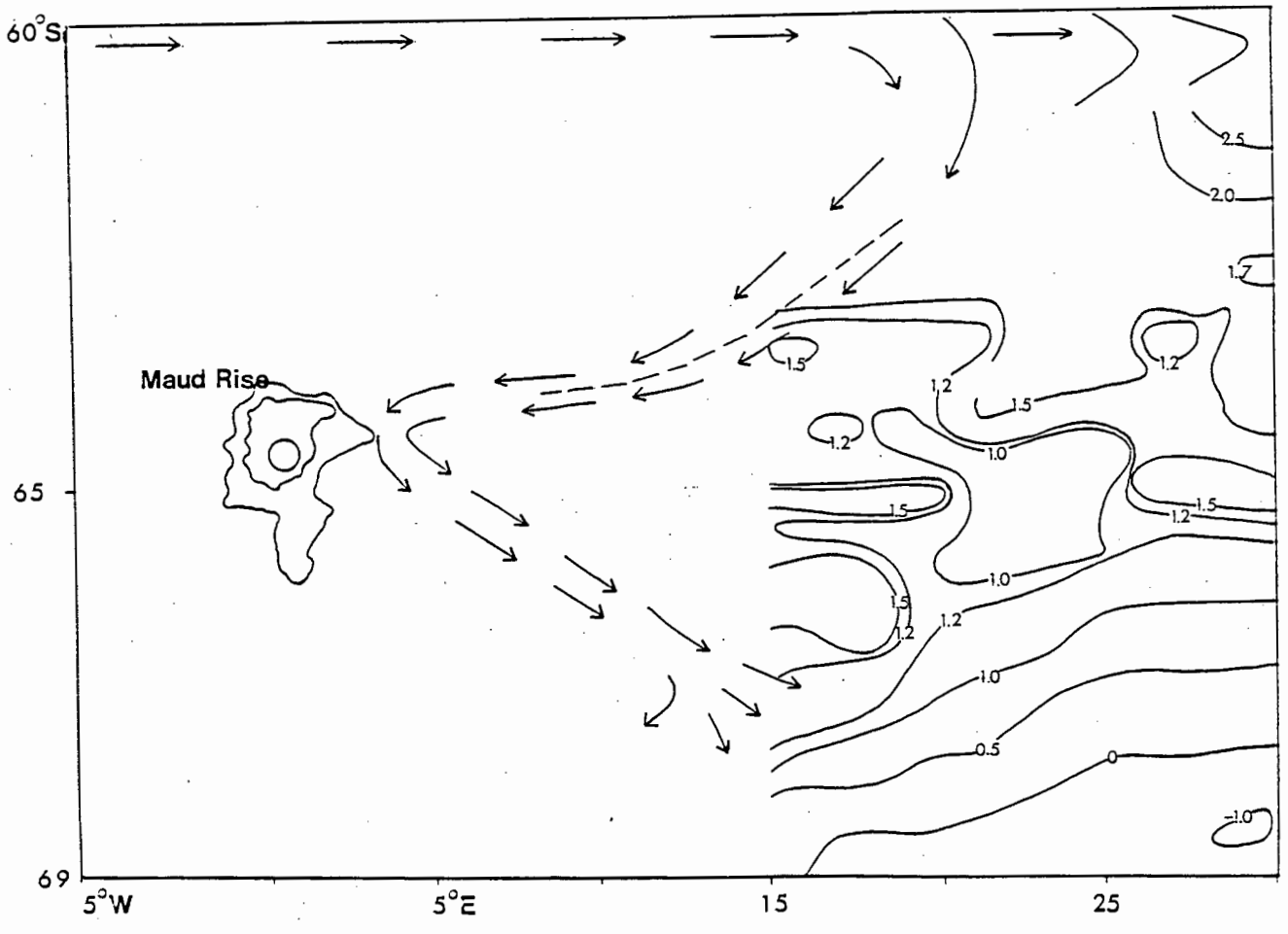


Fig. 5. The South African FIBEX survey area and vicinity with approximate position of the inter-gyral front (dashed line) postulated by Gordon and Huber (in press). A sea-surface temperature profile is presented for the area surveyed by South Africa during February-March, 1981, from data taken from the ship's log and physical data logged by Sea Fisheries Research Institute. The current flow (arrows) of the eastern Weddell Gyre and the anti-cyclonic gyre are from A.L. Gordon (pers. comm.).



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5.2.4. Agulhas Current Retroflection region

Relationships between seabirds and meso-scale hydrographic features in the Agulhas Current Retroflection region

Abstract. The species diversity, density and distribution of aerial seabirds in the Agulhas Current Retroflection region during November-December, 1983, are described in relation to meso-scale sea-surface habitat-types and circulation features resolved by real-time hydrography. The density of seabirds, especially species known to feed on plankton, correlates positively with cool water and thermohaline fronts. The diversity of seabird assemblages correlates positively with habitat-types which are characterized by sea-surface mixing processes (e.g. eddies).

Introduction

The macro-scale distribution of seabirds at sea reflects the biogeographical zonation of the marine habitat (Pocklington 1979, Griffiths et al., 1982; Section 5.1.1). The greatest densities of birds at sea occur within neritic and frontal zones (Ainley and Jacobs, 1981; Schneider, 1983; Section 5.1.2). In neritic and nearshore areas, seabird distribution is related to the positions of fronts and the oceanographic properties of habitat-types (Joiris, 1978, 1983; Schneider and Hunt, 1982; Schneider, 1983). However, it is not known how the distribution of seabirds is influenced by meso-scale sea-surface structure within a complex deep-sea mixing zone. This paper extends our understanding of the oceanographic determinants of pelagic seabird dispersion to a deep-sea area between the southern African continental shelf and the sub-Antarctic zone, where meso-scale features (e.g. eddies) are common (Lutjeharms, 1981).

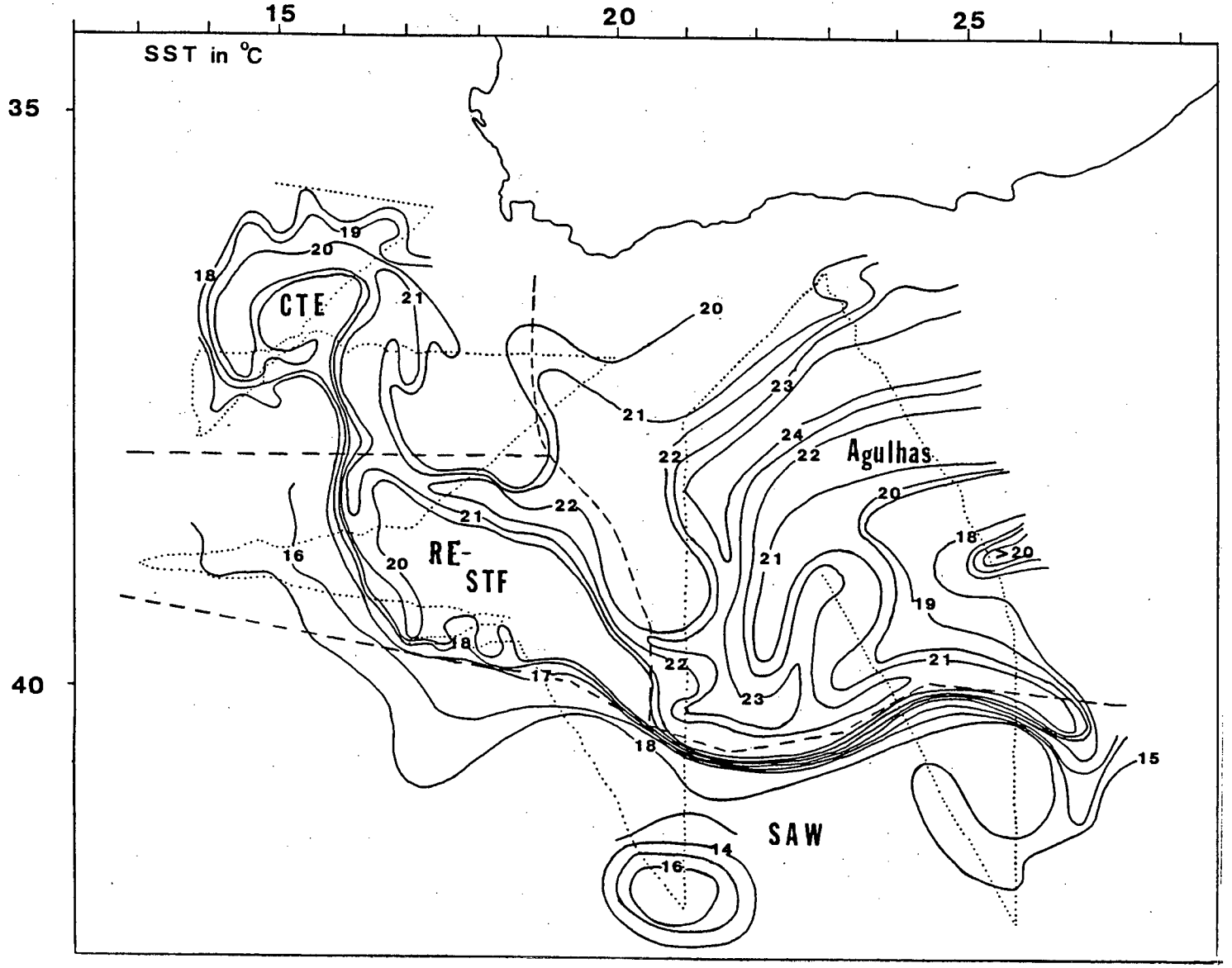
Methods

The Agulhas Retroflection Cruise (ARC) investigated the meso-scale hydrography of the area during November-December, 1983 (Gordon, in press). Concurrently, seabird distribution and density were assessed in relation to fronts, eddies, currents and current meanders in the interface region of the South Atlantic, Agulhas Current and Antarctic Circumpolar Current, and in a frontal zone previously termed the 'Sub-Tropical Convergence' (Deacon 1982). During the Agulhas Retroflection Cruise in the area between 35^{o}S and 42^{o}S latitudes and between 14^{o}and 27^{o}E longitudes (Fig. 1), seabirds observed flying past, or passed by, within 300 m abeam of

the R/V Knorr while steaming (mean vessel speed= 18 km h^{-1}), were counted, using the BIOMASS Seabird Mapping Scheme (10-minute observations, Anon., 1984). In my analyses, seabird species were lumped by principal diet-class: plankton- (PF), squid- (CF) and fish-eating species (FF), and species not readily classified (MF). Sea-surface temperature (SST), air temperature (AIR), salinity (SAL), barometric pressure (BAR), sea-surface oxygen values (OXY), wind speed (WINDS), weather (WEATH, coded 1 (clear, dry) to 6 (storm)) and solar radiation (RAD) were recorded at 2-3 minute intervals and coded for analysis at the interval of seabird counts. Identification of the sea-surface circulation features was based on XBT vertical sections (Lutjeharms, 1984).

Gordon (in press) identified discrete ocean circulation features based on measures of geostrophic flow (i.e. dynamic topography and potential temperature-salinity space diagrams) and satellite-tracked drifter buoys. The Cape Town Eddy was a mixture of South Atlantic central water and Agulhas South Indian Ocean water. The Cape Town Eddy received Agulhas water from the Retroflection Eddy. The latter eddy was shed from the Agulhas Current Retroflection and separated from it by a thermal front. The zone previously referred to as the 'Sub-Tropical Convergence' (Deacon, 1982) hereafter is referred to as the 'Sub-tropical Front' (STF), and was a steep thermohaline gradient separating Agulhas Current Retroflection water from sub-Antarctic boundary water. Based on these features, habitat-sectors defined for this analysis are: the Cape Town Eddy (CTE); the Retroflection Eddy and Sub-tropical Front (RE-STF); the Agulhas Current Retroflection system (Agulhas), and Sub-Antarctic water boundary (SAW) (Fig. 1). The breakdown of the cruise data into sectors was facilitated for cruise participants by A.L. Gordon (pers. comm.).

Fig. 1. The Agulhas Current Retroflection region showing sea-surface temperature (^{o}C), approximate positions (bounded by dashed lines) of CTE, RE-STF, Agulhas and SAW habitat-sectors (abbreviations as in text) and cruise-track (dotted lines) during November-December, 1983.



Seabird species richness and diversity for habitat-sectors were summarized by the Analysis of Alpha and Beta Diversity (Ter Braak, 1983), which is a species-centred bi-plot ordination analysis. In this analysis, the habitat-sectors with the highest diversity are plotted closest to the origin. The species or species-classes with the largest vectors pointing in the direction of the co-ordinates of a habitat-sector contribute most to the species diversity of that sector. A sector with low diversity has relatively few species with long vectors in its direction, and a sector with high diversity has a large number of species with shorter vectors (Ter Braak, 1983).

Cruise segments which crossed >300 km (16 h steaming at 18 km h^{-1}, or one day's steaming) were taken to reflect macro-scale seabird distribution (i.e. passage across one or more habitat-sectors). Cruise segments within a sector or across sector boundaries (fronts) were taken to reflect meso-scale distribution. The correlation of seabird density (no. individuals km^2) with the SST signatures of sea-surface features was performed by considering seabird counts as a Gaussian function of SST:

$$f(y) = P1 * e^{\frac{-(X-P2)^2}{2P3}} \qquad (1)$$

where P1 is a scalar value for bird density (y-axis), P2 (SST signature of sea-surface feature) is the SST associated with the peak in bird density, and P3 is a scalar parameter which represents the breadth of the peak of seabird density in terms of SST (x-axis). The curve parameter values (P1, P2, P3) were

determined by a computer program (BMDPAR, Dixon, 1981) which fits a curve through observed bird densities plotted against SST for each cruise-track segment. The equation derived was used to predict seabird density (y-values) for each SST (x-values) on that cruise segment. For each segment wherein seabird counts were stopped partway into an SST feature, the bird counts were transformed as a log + 1 function of SST. For each segment, the linear regression of the predicted (transformed) versus observed bird densities tested the hypothesis that seabird density increases up to, and decreases away from, the SST signature of a sea-surface feature. The values of P2 and P3 are not the same for different sea-surface features. Consequently, an approximate analysis of variance was used to establish that the composite of curvilinear model-runs provided a better fit to the data than the assumption that bird density and sea-surface temperature were independent (see Siegfried and Underhill (1975) for application of this test on biological data).

Results

Thirty-three (33) species of pelagic seabirds were recorded during the Agulhas Retroflection Cruise (ARC), of which 10 species accounted for > 85% of a total of 6,059 individuals (Appendix 1). Principal Components Analysis shows covariation among squid and fish eating species, so that species of these classes were lumped for further analysis (Appendix 2). Albatrosses and large petrels were correlated most strongly with avian biomass, species richness and diversity (Appendix 3). Prions Pachyptila spp. were correlated most strongly with avian density, but correlated most weakly with species richness and diversity (Appendix 3). The mixed-diet class comprised principally Softplumaged Petrels

Pterodroma mollis which co-occurred to some extent with prions (Appendix 2).

Macro-scale seabird distribution

Seabird density (all species) was greatest in areas of relatively cool SST and at thermohaline fronts (Fig. 2). Seabird density (all species) was correlated negatively with SST ($R=-0.62$, $P<0.05$). Plankton-eating birds correlated with cold air and high sea-surface oxygen values (Table 1), both of which correlated with cold SST ($R=0.55$, $R=0.94$, respectively, $P<0.01$). Piscivores generally correlated with warm environmental conditions typical of the African continental shelf (can. var. 3, Table 1). Squid-eating seabirds were most abundant in the absence of planktivores and piscivores and over cold water, when the air was cold and barometric pressure was low (can. var. 2, Table 1). During ARC, the passage of a cold-weatner front was encountered (i.e. low temperatures, low barometric pressure, strong winds and wet weather). The absence of planktivores and relative abundance of species which take squid and mixed-diets during this storm is reflected in canonical variate 2 (Table 1).

Meso-scale seabird distribution

The species composition and density of pelagic seabirds differed by habitat-sectors (Table 2). Ter Braak's (1983) diversity bi-plots (Fig. 3) showed that the greatest differences in avian species composition occurred between the Agulhas and sub-Antarctic water (SAW) sectors. The Agulhas sector contained nutrient-poor, warm surface water, in contrast to the nutrient-rich, cold surface waters of the SAW sector (Figs 1 and 4). The Agulhas sector contained principally piscivores, with some squid-eating and

mixed-diet species (Table 2, Fig. 3). The SAW sector was dominated by planktivores (mainly prions) in density (Fig. 3), but this is partly due to very large flocks of prions suppressing the statistical importance of more normal-sized bird aggregations. When the bird density data were log-transformed, the diversity bi-plot reflected more realistically the contribution to each habitat-sector of bird species other than those which were numerically dominant.

Extensive horizontal mixing was evident from the patchiness of surface nutrients in the RE-STF and CTE sectors (Fig. 4). Squid-eating seabirds and species which take mixed-diets provided relatively high avian diversity in the RE-STF and CTE sectors (Fig. 3). These birds accounted for particularly high avian biomass where the surface waters of the Retroflection Eddy (ca. 19°C) and the Sub-tropical Front (ca. 17°C) were pushed close together in a current meander (Table 2). In general, the short vectors for the squid-eating albatrosses and petrels should be noted, as they were the most widespread seabirds (Table 2, Fig. 3). The mixed-diet species were also widespread (Fig. 3).

The survey recrossed both the Retroflection and Cape Town eddy sectors within one month. The seabird data for each crossing of the eddies were ordered as an approximate 'time series' representing possible phases of eddy development. The Retroflection Eddy originated at the Agulhas Current Retroflection (apparently not long before the first crossing), and later (i.e. the second crossing) was separated from the Agulhas Current by a northward intrusion of cold water. Long-term transfer of Agulhas water from the Retroflection Eddy fed the development of the Cape Town Eddy. Subsequent to the first crossing, the warm Agulhas

Fig. 2. The distribution and density (no. individuals km^2) of seabirds (all species) in relation to sea-surface temperature (as in Fig. 1) in the Agulhas Current Retroflection region during November-December, 1983.

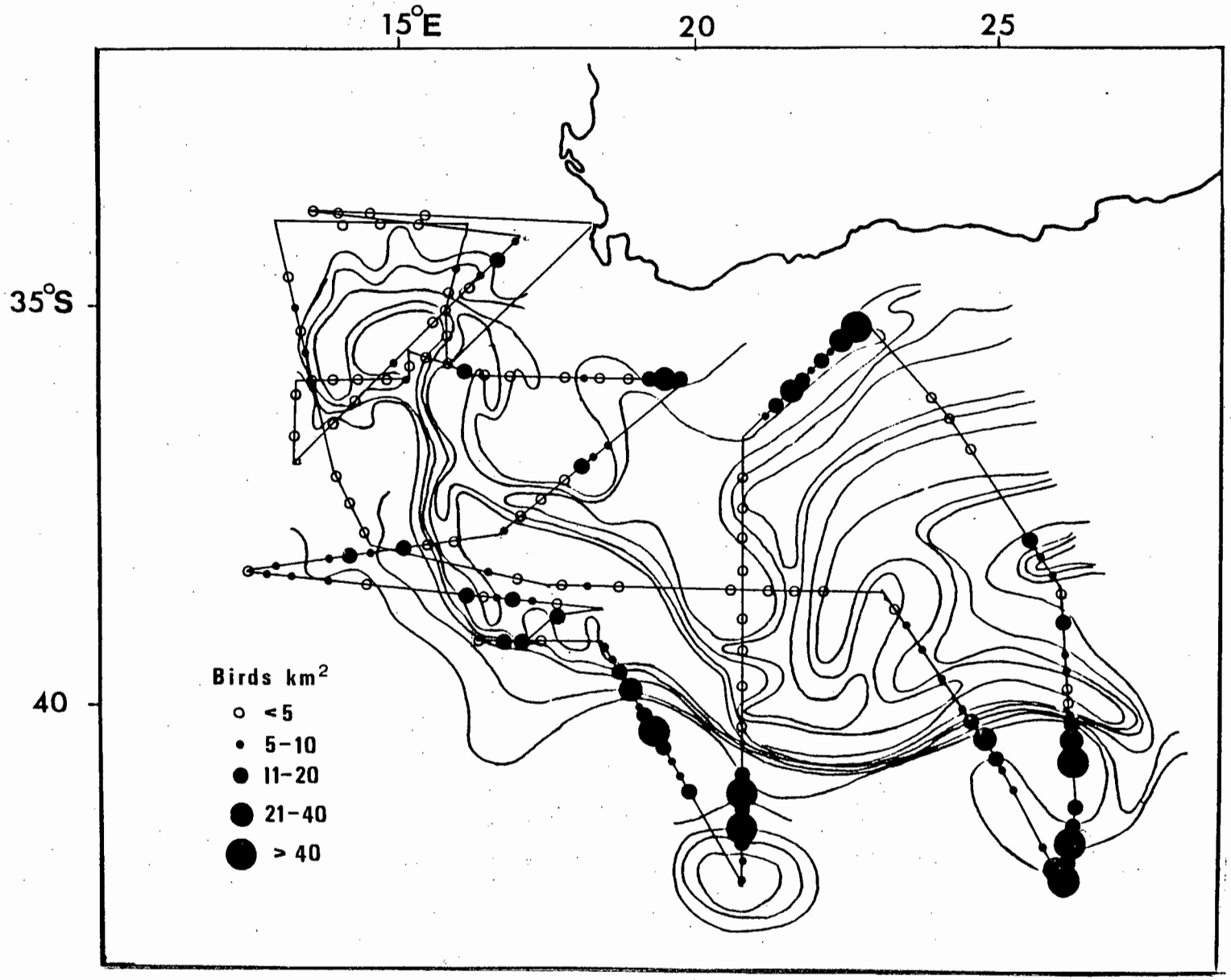
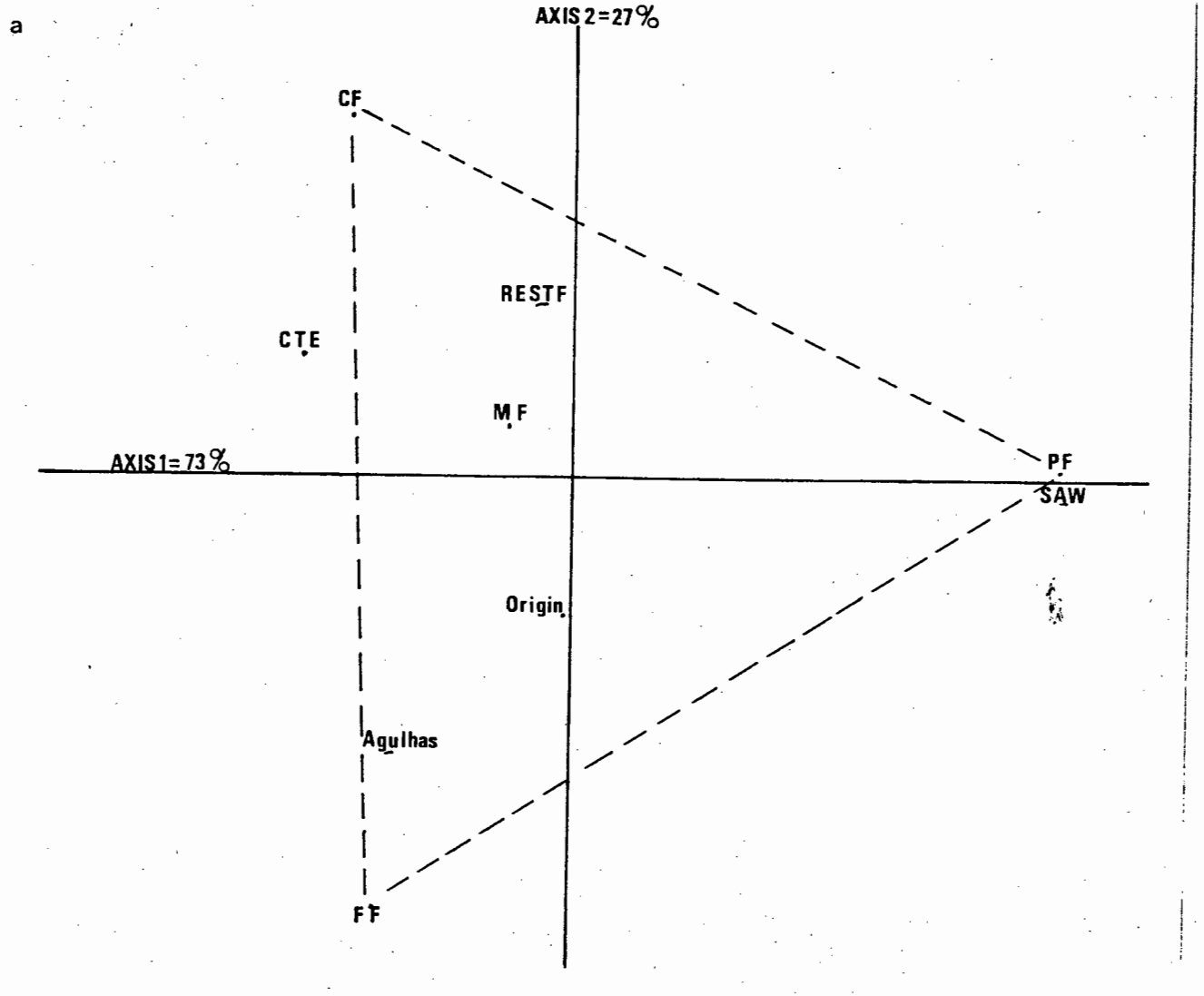
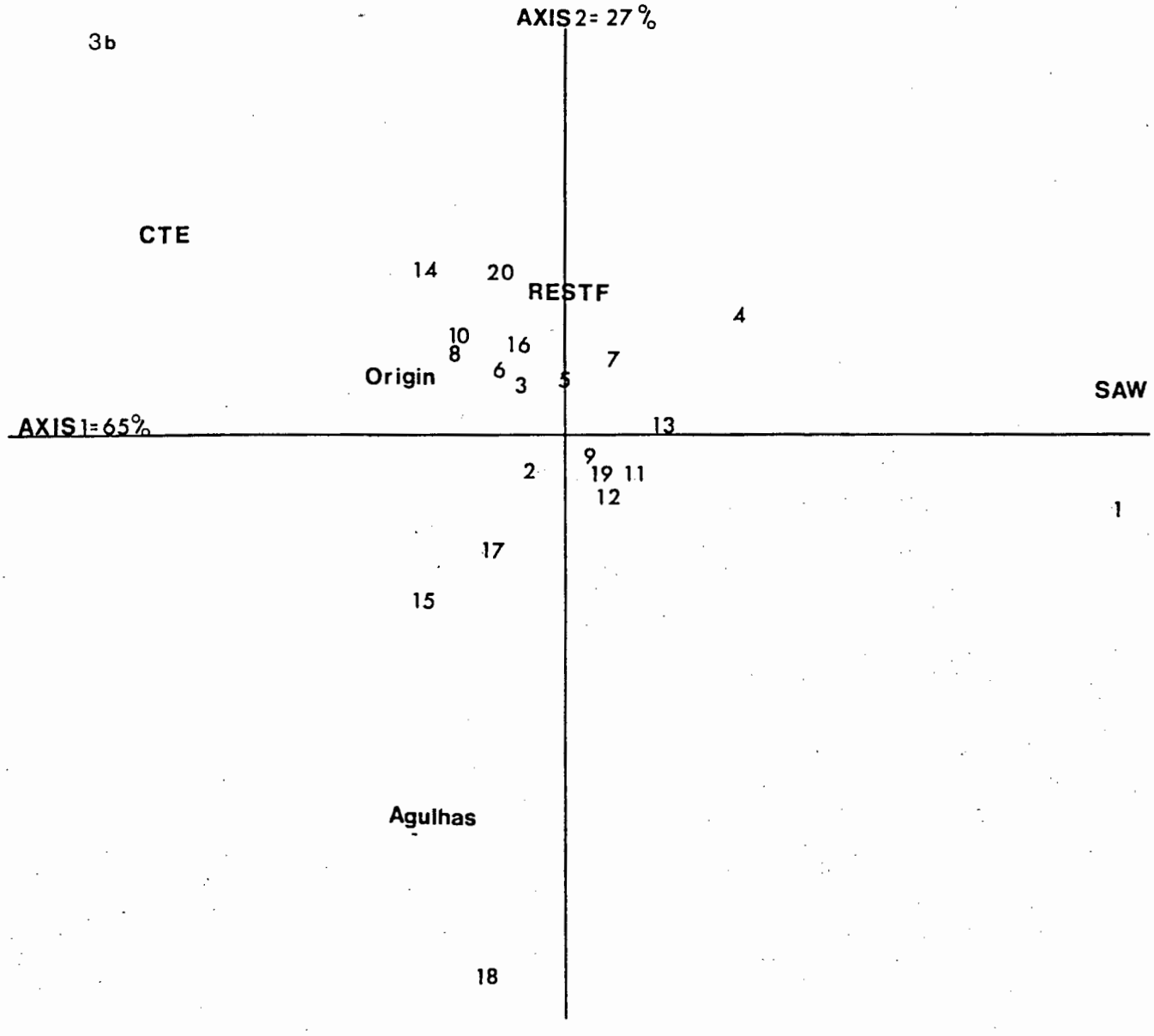


Fig. 3. Ter Braak's (1983) diversity bi-plots showing species diversity for the habitat-sectors in the Agulhas Current Retroflection region during November-December, 1983, in terms of mean densities (no. individuals km^2) of (a) seabird diet-classes, and (b) the log-transformation of seabird species. Abbreviations for diet-classes are given in the text. Pachyptila spp. (1), Oceanites oceanicus (2), Oceanodroma leucorhoa (3), Fregetta tropica (4), Fregetta grallaria (5), Diomedea exulans (6), Diomedea melanophris (7), Diomedea chlororhynchos (8), Diomedea cauta (9), Pterodroma macroptera (10), Pterodroma lessonii (11), Procellaria aequinoctialis (12), Procellaria cinerea (13), Puffinus gravis (14), Calonectris diomedea (15), Puffinus griseus (16), Sterna vittata (17), Sterna paradisaea (17), Sterna hirundu (17), Morus capensis (18), Pterodroma mollis (19), Stercorarius longicaudus (20).




AXIS 2= 27 %
3b
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SAW
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12
1
17
15
Agulhas
18

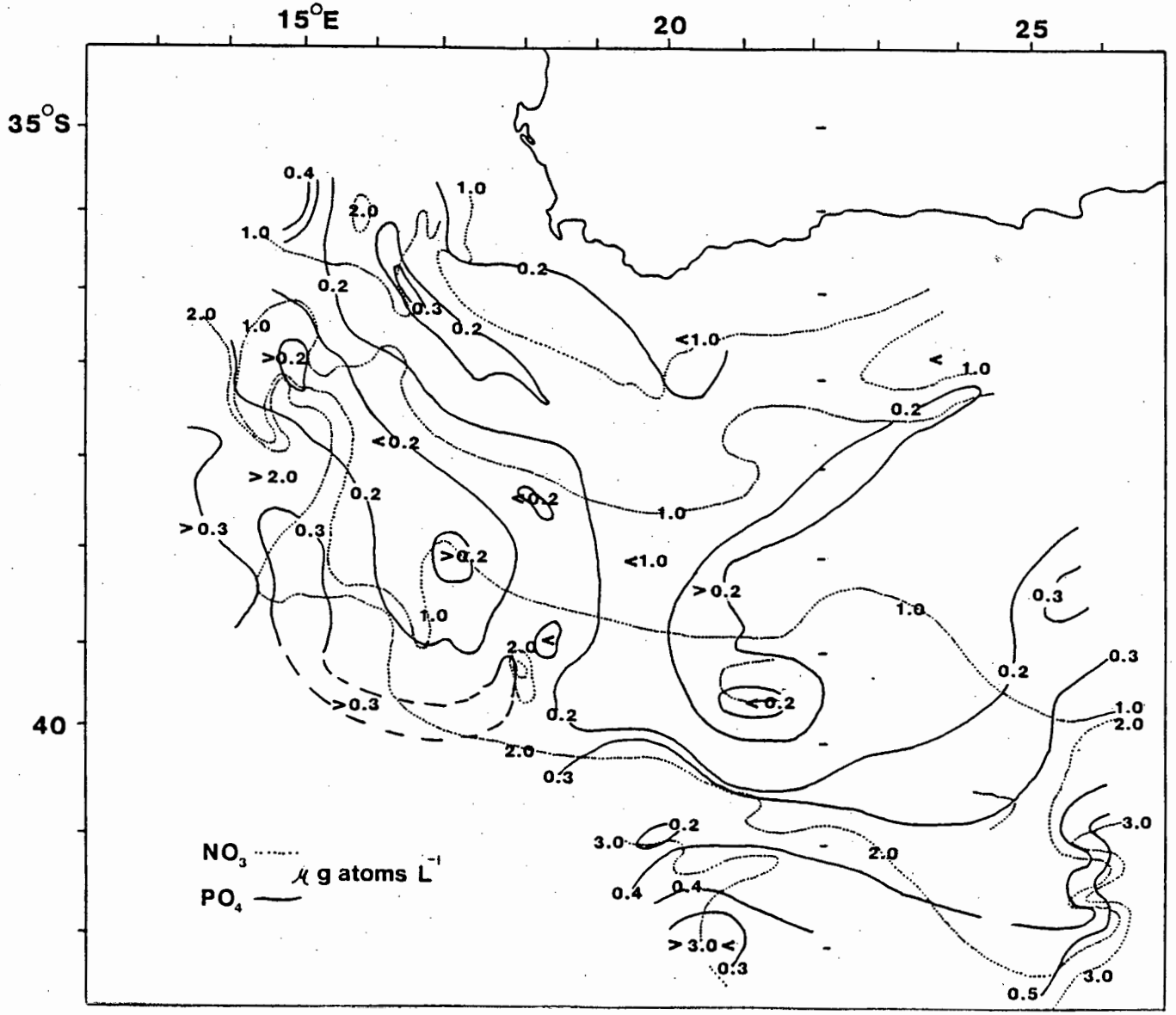
Table 1. Coefficients of determination (R^2) and variable loadings from canonical correlations between seabird density (no. individuals km^2) by diet-class and environmental variables in the Agulhas Current Retroflection region, November-December 1983. Variable abbreviations as in text.

Variables	Canonical variate loadings			
Seabird diet-class	1	2	3	4
PF	0.779	-0.629	0.006	-0.435
CF	0.007	0.763	0.103	-0.717
FF	-0.329	-0.423	0.866	-0.102
MF	0.254	0.390	0.581	0.824
Environment				
BAR	0.140	-0.713	-0.051	-0.126
SAL	0.040	0.330	-0.356	0.231
AIR	-0.572	-0.607	0.556	-0.712
WAT	0.253	-0.582	-0.191	3.198
WINDS	-0.097	0.444	0.695	0.029
WEATH	0.177	0.074	-0.133	-0.239
OXY	0.705	-0.756	0.313	2.561
RAD	0.170	0.076	-0.643	-0.085
R	0.50	0.15	0.09	0.02
P<	0.01	0.01	0.01	0.05

Table 2. Means and their standard deviations (in brackets) of bird species richness (BSR), bird species diversity (BSD), biomass (live-weight) and density (no. individuals km^2 (TOT)) of four seabird diet-classes (abbreviations as in text) for four habitat sectors (abbreviations as in text). The differences between the habitat-sectors are significant ($P<0.01$) for all variables. Data are for the entire Agulhas Retroflection Cruise, November-December, 1983

Sector	N	BSR	BSD	MASS	PF	CF	FF	MF	TOT
CTE	140	1.61	0.42	2.82	0.1	1.3	0.4	0.7	2.5
		(1.30)	(0.48)	(4.51)	(0.4)	(1.7)	(0.9)	(1.3)	(2.6)
RE-STF	184	3.13	0.89	8.86	1.5	2.8	0.3	1.7	6.2
		(1.81)	(0.58)	(8.98)	(3.4)	(2.6)	(0.6)	(3.3)	(6.0)
SAW	128	4.48	1.10	8.92	14.4	3.3	0.3	4.3	22.3
		(1.68)	(0.45)	(6.14)	(26.9)	(3.1)	(1.0)	(3.8)	(27.4)
Agulhas	182	2.22	0.55	9.45	0.8	1.7	3.0	1.8	7.3
		(1.69)	(0.53)	(21.68)	(3.8)	(2.5)	(9.7)	(3.1)	(11.7)

Fig. 4. The surface distribution of nutrients (NO_3, PO_4) in the Agulhas Current Retroflection region during November-December, 1983.



water was mixed with Atlantic water within the Cape Town Eddy (second crossing) (Gordon, in press). Seabird diversity and density decreased as the 'time series' of eddy development progressed (Fig. 5). Significant differences occurred (Chi-Square test, $P<0.001$) in the densities and relative proportions (diversity) of the birds lumped by diet-classes for the early and late crossings of the RE ($\chi^2=24.66$) and the CTE ($\chi^2=29.33$) (Fig. 5). The differences of seabird diet-class diversity and density between the CTE and the RE were most pronounced ($\chi^2=52.69$, $P<0.001$, Fig. 5).

Seabird-SST correlations

Seabird density was correlated positively with SST signatures of thermohaline fronts, which occurred along eddy rims and habitat-sector boundaries (Fig. 2, Appendix 4). Piscivorous and planktivorous seabirds were correlated with warm (SST>21^{o}C) and cold (SST<17^{o}C) fronts, respectively (Figs 2 and 6). Generalist avian predators, i.e. squid-eaters and species which take mixed diets, were correlated with diverse frontal conditions, particularly SST's between 18^{o} C and 21^{o}C (Figs 2 and 6). The density of the combined diet-classes was the best correlate of the SST signatures of the series of thermal gradients which comprised the STF zone (SST= 14-18^{o}C, Figs 2 and 6).

Seven out of 18 meso-scale segments across fronts produced non-linear correlations between seabird density and SST with $R>0.70$ (Fig. 6, Appendix 4). The association between seabird density and SST was strongest over colder water (Figs 6 and 7). For the composite of all meso-scale correlations (Appendix 4), the variance explained by the curvilinear model was significantly greater than for a model assuming independence of birds and SST (Table 3). Surprisingly, there was not a good correlation between

bird density and change in SST (per 10 minute field card or multiples of them). However, where seabirds were aggregated at SST fronts, there were also steep gradients in the dynamic topography of the sea surface relative to the 1500db/10^{o}C plane (compare Fig. 2 with Fig. 2 in Gordon, (in press)). Softplumaged Petrel aggregations were more closely associated with the dynamic topography gradients than with SST fronts.

Table 3. Analysis of variance to determine the overall significance of the correlations between observed seabird densities (no. individuals km^2) and seabird densities predicted by the curvilinear regressions with SST (Appendix 4) for the Agulhas Current Retroflection region during November-December, 1983.

Scale of analysis		d.f.	SS	MS	F	Prob.
Macro-scale	Regression	21	27937	1330		
	Residual	309	63214	205	6.49	0.01
	Total	330	91151			
Meso-scale	Regression	57	29214	513		
	Residual	313	33212	106	4.84	0.01
	Total	370	62426			

Fig. 5. Percentage density (no. individuals km^2) of seabird diet-classes for the two crossings of the Cape Town Eddy (CTE) and the Retroflection Eddy (RE) showing time between crossings (x-axis). The differences in the seabird diet-class diversity and density observed during the recrossings of each eddy, and the differences in the avifauna between the CTE and RE, are significant by Chi-Square test. Mean number of individuals per km in plankton (open bar), squid (black bar), fish (hatched bar) and mixed-diet (stippled bar) classes are shown above histograms.

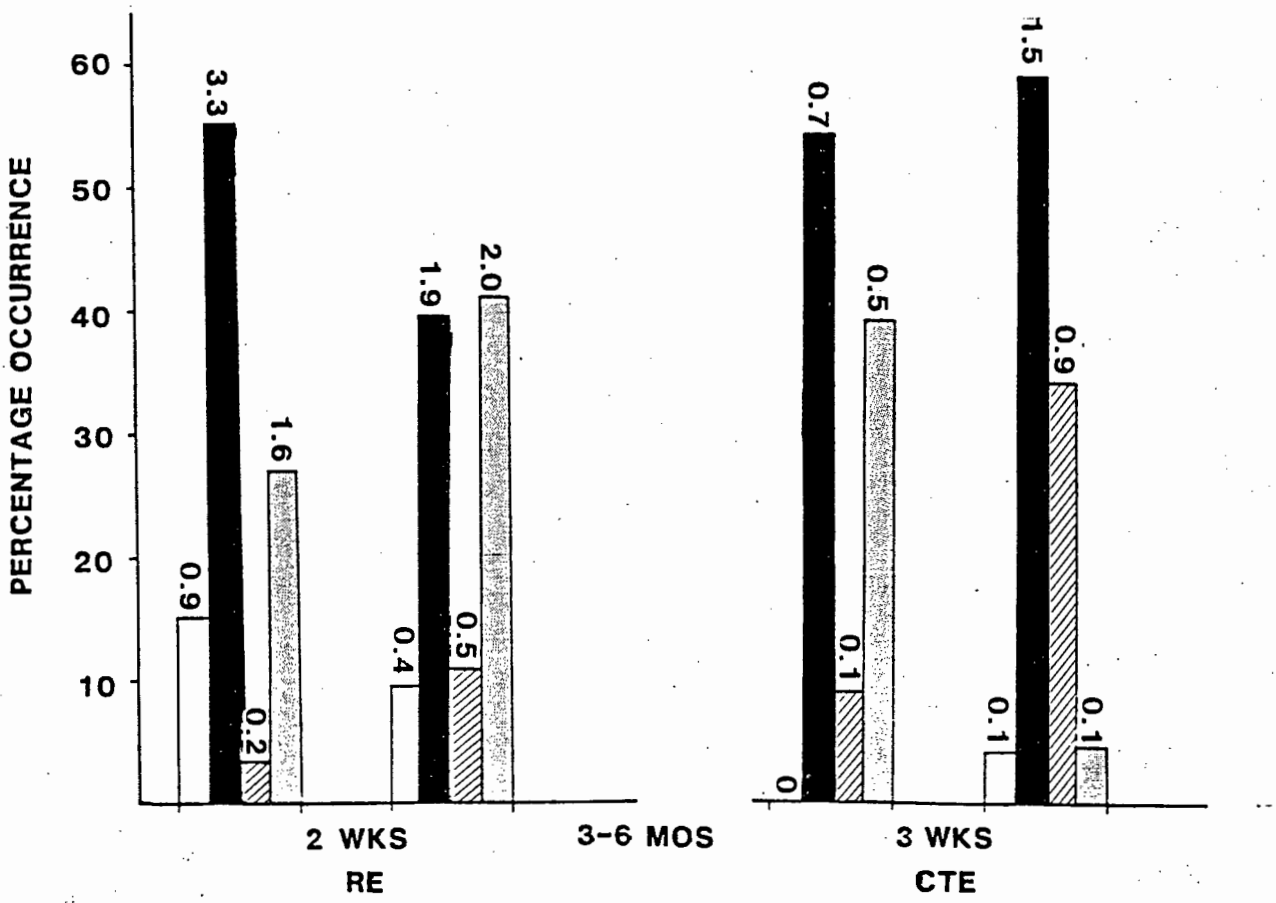


Fig. 6. Coefficients of correlation (R) between observed and predicted seabird densities (no. individuals km^2) in relation to SST signatures of fronts (P2) on 26 cruise segments (Appendix 4) in the Agulhas Current Retroflection region during November-December, 1983. The seabird variable used in each run of the predictive model is denoted as: plankton- (P), squid- (C), fish- (F) and mixed-diet species (M) or all species (T). Results from macro-scale cruise segments are circled, meso-scale segments are not.

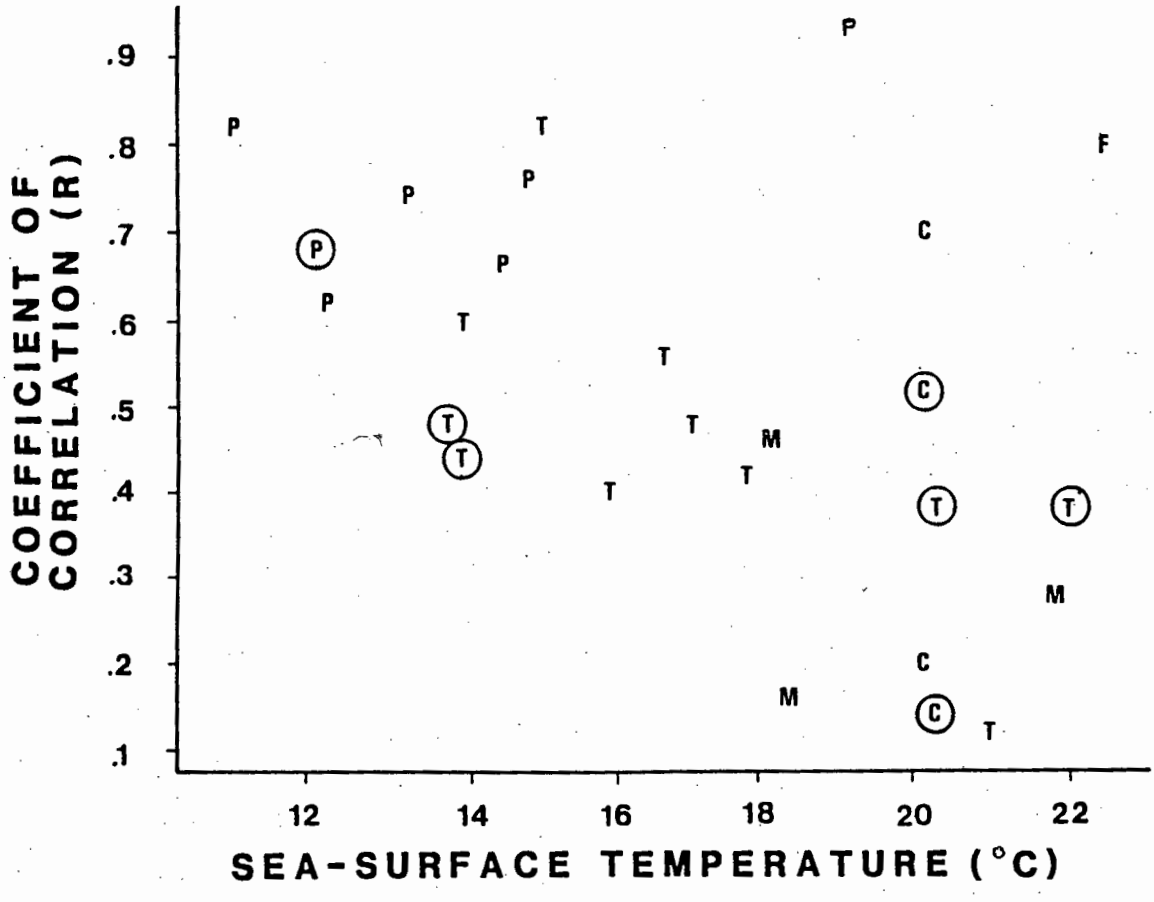
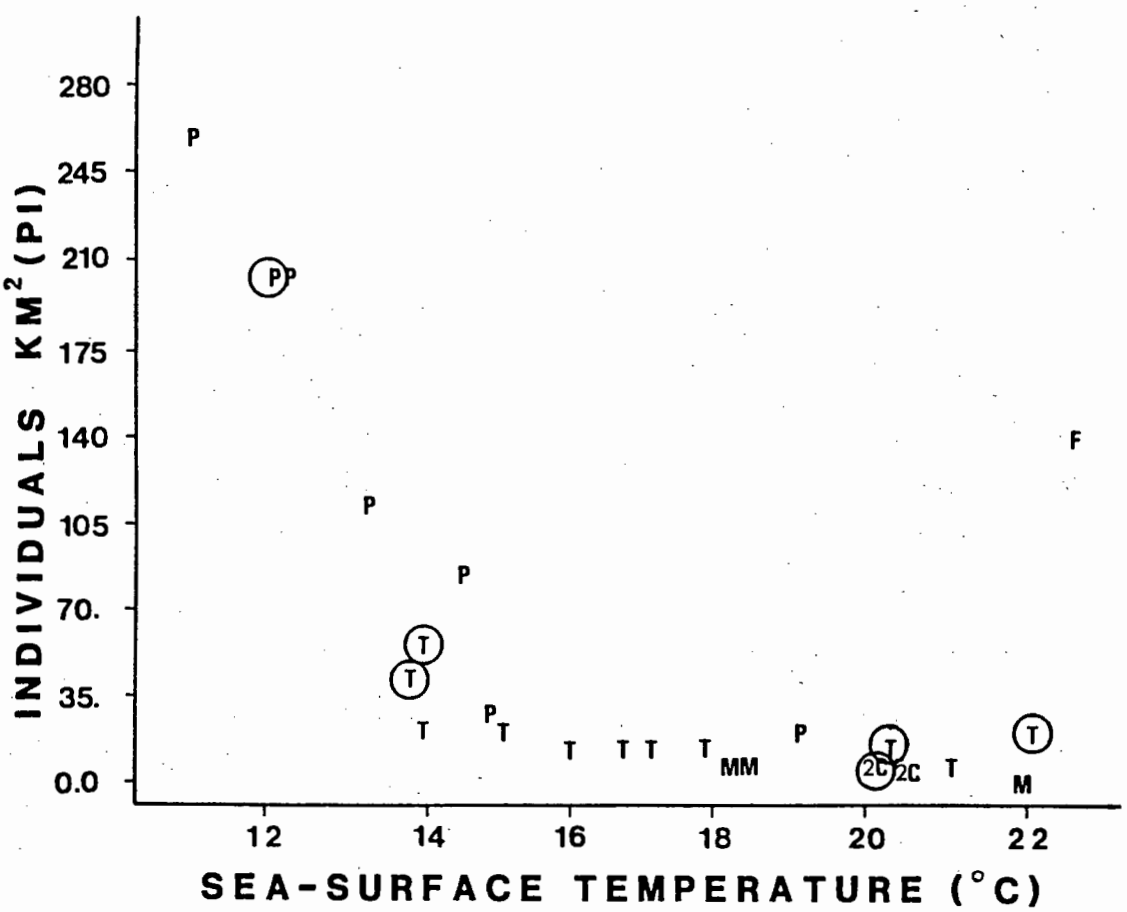


Fig. 7. The relationship between mean predicted seabird density (no. individuals km^2) (P1) and SST (P2) for the 26 cruise segments modelled in Fig. 6, in the Agulhas Current Retroflection region during November-December, 1983. Abbreviations as in Fig. 6.



Discussion

The seabird assemblages observed in each of four meso-scale habitat-types were different in terms of species diversity and density. Hence, this study supports the generalization that meso-scale habitat-structure influences the composition of seabird assemblages in deep-sea areas, (Section 5.2.1), as occurs in nearshore environments (Joiris, 1978, 1983; Schneider and Hunt, 1982). Generalist avian predators were associated with eddies, perhaps because mixing processes inherent in ocean eddies enhance prey diversity and availability (Tranter et al., 1983). Conversely, specialist avian predators were relatively acute indicators of the Sub-tropical Frontal zone (Section 5.1.2), a biologically productive boundary zone between two biogeographical regimes (see Section 5.2.2).

Generally, seabird distribution and density correlate positively with the cooler waters of the area surveyed during ARC (Section 5.1.2). It is possible that the observed differences between seabirds associated with the CTE and the RE were due to the proximity of the RE to the STF, or to the fact that the RE core was cooler than that of the CTE. However, it is also possible that differences in these avifauna reflected biological changes generally found during the transfer of Agulhas water to the area of the CTE. If the seabirds were tracking their environment on a meso-scale, then the occurrence of a largely squid-eating avifauna over the CTE could possibly indicate that 'older' eddies contain a proportionately lower abundance of primary consumers (i.e. plankton), relative to secondary consumers (i.e. squid and fish). Data on prey distribution are needed to confirm this. Such a finding could facilitate understanding of the spatio-temporal

cycles involved in ecological succession in eddies.

Macro- and meso-scale oceanic features were equally significant correlates of seabird density. Curvilinear correlations between fronts (indicated by SST) and seabird abundance were stronger than in previous studies which relied on linear regression models and scales of hydrography which were probably too coarse to resolve meso-scale, sea-surface features (Kinder et al., 1983; Section 5.1.2). Taking together all of the macro- and meso-scale correlations, the variance in seabird density explained by sea-surface temperature patterns was statistically significant.

The attraction of seabirds to fronts could be based in part on temperature sensing (Schneider, 1983; Section 5.1.2). However, correlations between seabirds and rate of change in SST were weak, indicating that seabirds probably use a variety of cues to locate prey (Section 5.1.2). Seabirds are attracted to and avoid a variety of meteorological conditions (Manikowski, 1971; Mendelsohn, 1981; Section 5.2.1). In the case of Softplumaged Petrels, some of the variance unaccounted for by associations with SST fronts may be partially explained by the birds' response to baroclinic gradients, which correspond closely, but not entirely, with SST fronts. It is possible that seabirds see current-jets, such as currents of 2 knots and greater, which occurred along the baroclinic and thermohaline gradients surrounding the cores of the eddies and of the Agulhas Current Retroflection (Gordon, in press).

The regression model developed in this study linking seabird density with sea-surface temperature fronts describes a tendency for birds to aggregate at oceanic fronts. It is important to note that a generalized model is not now possible because the

characterisitics (e.g. SST) to which the birds seem to respond differ with season and geographical location (Section 5.1.2). For particular regions or habitat-types the species composition of seabird assemblages, and the strength of associations between bird densities and the fronts, can be anticipated if the sea-surface structure is known. Thus, predictive application of my descriptive model requires real-time hydrology concurrent with seabird counts. Future research should aim at adding parameters which complement sea-surface temperature to the regression models, thereby increasing our understanding of the multiple cues to which seabirds respond.

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Appendix 1. Principal food-type and feeding-method classes, body-mass (live-weight) and percentage abundance (number of individuals) of species observed in the Agulhas Current Retroflection region during November-December, 1983. Diet and feeding-method classifications based on data in Ashmole (1971) and unpublished records taken from the FitzPatrick Institute, which also maintains records of bird weights.

			kg	%
Plankton	Surface-filter	Pachyptila spp, prions	0.15	28.87
	Dip/patter	Oceanites oceanicus, Wilson's Stormpetrel	0.04	2.02
	"	Oceanodromia leucorhoa, Leach's Stormpetrel	0.05	0.11
	"	Fregetta tropica, Blackbellied Stormpetrel	0.06	4.75
	"	Fregetta grallaria, Whitebellied Stormpetrel	0.05	0.58
	"	Phalaropus fulicarius, Grey Phalasope	0.03	0.10
				36.43
Squid	Surface seize/scavenge	Diomedea exulans, Wandering Albatross	8.60	2.97
	"	Diomedea melanophris, Blackbrowed Albatross	3.50	4.38
	"	Diomedea chrysostoma, Greyheaded Albatross	3.60	0.07
	"	Diomedea chlororhynchos, Yellownosed Albatross	2.00	2.10
	"	Diomedea cauta, Shy Albatross	4.10	0.91
	"	Phoebetria fusca, Sooty Albatross	2.50	0.03
	"	Phoebetria palpebrata, Light-mantled Sooty Albatross	2.70	0.03
	"	Daption capense, Pintado Petrel	0.45	0.58
	"	Pterodroma macroptera, Greatwinged Petrel	0.58	6.73
	"	Pterodroma lessonii, Whiteheaded Petrel	0.75	0.53
	"	Pterodroma incerta, Atlantic Petrel	0.52	0.08
	"	Procellaria aequinoctialis, Whitechinned Petrel	1.21	7.53
	"	Procellaria cinerea, Grey Petrel	1.03	0.69
	Pursuit plunge	Puffinus gravis, Great Shearwater	0.95	1.58
				28.21

Fish	Surface seize/scavenge	Calonectris diomedea, Cory's Shearwater	0.96	2.33
	Pursuit plunge	Puffinus griseus, Sooty Shearwater	0.79	1.81
	Surface seize/scavenge	Puffinus assimilis, Little Shearwater	0.23	0.23
	Dip/patter	Sterna vittata, Antarctic tern	0.14	1.37
	"	Sterna paradisaea, Arctic tern	0.13	0.55
	Plunge	Morus capensis, Cape Gannet	2.70	5.46
	Dip/patter	Sterna hirundu, Common Tern	0.15	1.37
				13.12
Mixed	Surface seize/scavenge	Macronectes giganteus, Southern Giant Petrel	4.10	0.52
	"	Pterodroma mollis, Softplumaged Petrel	0.31	20.28
	Piracy	Catharacta antarctica, Sub Antarctic Skua	1.63	0.12
	"	Stercorarius pomarinus, Pomasines Skua	0.67	0.03
	"	Stercorarius parasiticus, Arctic Skua	0.53	0.11
	"	Stercorarius longicaudus, Longtailed Skua	0.29	1.09
				22.15

Appendix 2. Principal components analysis showing co-occurrences among seabird species observed in the Agulhas Current Retroflection region during November-December, 1983. Abbreviations of species names are the first one or two letters of the genus and species names given in Appendix 1.

	PC1	PC2	PC3	PC4	PC5	PC6
DM	0.794	0.000	0.000	0.000	0.000	0.000
DCA	0.785	0.000	0.000	0.000	0.000	0.000
PRA	0.707	0.000	0.000	0.000	0.000	0.000
SC	0.000	0.744	0.000	0.000	0.000	0.000
STH	0.000	0.712	0.000	0.000	0.000	0.000
CD	0.000	0.540	0.000	0.000	0.000	0.000
PRC	0.000	0.000	0.687	0.000	0.000	0.000
PTM	0.000.	0.000	0.642	0.453	0.000	0.000
PAC	0.000	0.000	0.589	0.000	0.000	0.000
PTM	0.000	0.000	0.000	0.572	0.000	0.000
DC	0.000	0.000	0.000	0.546	0.000	0.000
HY	0.000	0.000	0.269	0.519	0.000	0.000
PTMM	0.000	0.000	0.000	0.000	0.697	0.000
PUGA	0.000	0.000	0.000	0.000	0.579	0.300
DCL	0.000	0.000	0.000	0.000	0.000	0.671
PU	0.000	0.000	0.000	0.000	0.000	0.530
FRT	0.000	0.000	0.000	0.000	0.000	-0.386
PUGI	0.000	0.000	0.000	0.000	0.270	0.000
MA	0.000	0.272	0.000	0.475	0.000	0.000
PTI	0.000	0.000	0.000	0.000	0.281	0.350
DCR	0.000	0.000	0.000	0.000	0.000	0.000
OO	0.000	0.303	0.000	0.000	0.000	0.000

PTL	0.000	0.000	0.257	0.000	0.306	-0.324
DMC	0.282	0.000	0.269	0.000	0.433	0.000

Appendix 3. Coefficients of correlation (r) showing interdependencies among seabird variables in the habitat-sectors CTE, RE-STF, Agulhas and SAW in the Agulhas Current Retroflection region during November-December, 1983. Abbreviations for habitat-sectors and seabird variables are given in text. The abundance variables were log-transformed for these regressions due to the preponderance of zero counts.

CTE

	BSR	BSD	TOT	MAS	PF	CF	FF
BSR	1.0000						
BSD	0.9337	1.0000					
TOT	0.9238	0.8047	1.0000				
MAS	0.8185	0.7137	0.8209	1.0000			
PF	0.2707	0.2674	0.2541	0.0253	1.0000		
CF	0.7391	0.6514	0.7786	0.8005	0.0687	1.0000	
FF	0.3366	0.2790	0.3339	0.2568	-0.0543	0.0637	1.0000
MF	0.5814	0.5532	0.5698	0.3767	0.1950	0.2163	-0.1419

RE-STF

	BSR	BSD	TOT	MAS	PF	CF	FF
BSR	1.0000						
BSD	0.9556	1.0000					
TOT	0.8776	0.7631	1.0000				
MAS	0.6990	0.6579	0.6919	1.0000			
PF	0.5329	0.4494	0.6267	0.2023	1.0000		
CF	0.7729	0.7518	0.7442	0.8160	0.2106	1.0000	
FF	0.3199	0.3205	0.2386	0.0964	0.0425	0.1455	1.0000
MF	0.4786	0.3854	0.5352	0.2207	0.2811	0.1411	0.0293

AGULHAS

	BSR	BSD	TOT	MAS	PF	CF	FF
BSR	1.0000						
BSD	0.9408	1.0000					
TOT	0.8877	0.7566	1.0000				
MAS	0.8347	0.7415	0.8436	1.0000			
PF	0.4755	0.4610	0.4029	0.2104	1.0000		
CF	0.7577	0.7319	0.6352	0.6792	0.1329	1.0000	
FF	0.4399	0.3655	0.4892	0.5831	0.1279	0.1265	1.0000
MF	0.3769	0.2915	0.4675	0.1489	0.1888	0.2856	-0.3769

SAW

	BSR	BSD	TOT	MAS	PF	CF	FF
BSR	1.0000						
BSD	0.7376	1.0000					
TOT	0.4540	-0.0751	1.0000				
MAS	0.5993	0.2919	0.5985	1.0000			
PF	0.2582	-0.2045	0.7809	0.2836	1.0000		
CF	0.6807	0.5556	0.3607	0.6776	-0.0551	1.0000	
FF	0.4411	0.4224	0.1579	0.2084	0.0941	0.2427	1.0000
MF	0.3085	0.1553	0.3681	0.3352	-0.0650	0.3986	0.0813

Appendix 4. Curvilinear correlations between seabird density (no. individuals km^2) and SST (^oC) for 26 cruise-track segments in the Agulhas Current Retroflection region during November-December, 1983, showing type of sea-surface feature (spatial scale in brackets), location (abbreviations as in text), seabird variable modelled (abbreviations as in text), sample size (N), mean predicted density (P1, no. individuals km^2), SST signature of feature (P2,^oC), and regression coefficient (R) between observed and predicted seabird densities.

Feature	Location	Seabird variable	N	P1	P2	R
Eddy rim	:CTE	TOT	29	4.1	21.1	0.13
(meso-scale)	:SAW	PF	21	28.4	14.9	0.75
Across neritic-						
deep-sea	: west	CF	34	4.8	20.4	0.14
boundary	Agulhas bank	FF	34	log+1	19.3	-0.47
(macro-scale)	: east	TOT	44	22.4	22.1	0.39
	Agulhas bank					
In neritic						
zone	: east	FF	26	136.7	22.5	0.79
(meso-scale)	Agulhas bank					
Across STF zone: (macro-scale)						
	14^oE	TOT	45	log+1	13.0	-0.35

	17-18°E	TOT	31	9.1	20.3	0.39
	17-18°E	CF	31	6.4	20.2	0.53
	20-21°E	PF	54	200.0	12.1	0.68
	20-21°E	PF	33	log+1	13.0	-0.69
	24-26°E	TOT	83	41.0	13.8	0.47
	26°E	TOT	53	54.9	14.1	0.43
In STF zone: (meso-scale)						
RE,STF meanders:	18°E	CF	16	4.6	20.1	0.20
	18°E	MF	16	3.0	22.0	0.27
	18°E	CF	15	6.1	20.2	0.70
	18°E	MF	15	5.0	18.4	0.16
Mid-STF:	19°E	TOT	21	13.0	17.8	0.42
	19°E	MF	21	8.3	18.1	0.45
	26°E	PF	26	log+1	16.0	-0.57
	24°E	TOT	30	15.0	17.1	0.48
	24°E	PF	30	22.7	19.0	0.91
STF,SAW interface:	15°E	TOT	17	14.9	16.7	0.56
	15°E	TOT	16	11.3	16.1	0.40
	15°E	TOT	20	23.1	15.1	0.82
In SAW zone:(meso-scale)	14°E	TOT	14	21.2	14.0	0.59
	20°E	PF	21	261.5	11.0	0.81
	20°E	PF	17	200.0	12.3	0.61
	21°E	PF	12	114.8	13.3	0.73
	26°E	PF	14	81.7	14.6	0.67

6. Synthesis and conclusion

6.1. Synthesis of results

There is consensus that, in neritic areas, aerial seabirds concentrate where fish, squid and plankton are most abundant at the sea-surface (Brown, 1980; Hunt et al., 1981; Croxall, 1984). In this study, I show that the deep-sea distribution of non-breeding seabirds in the Southern Ocean reflects the structure of the marine habitat. If seabird prey are ordered similarly, then my reults reflect the corollary that seabird assemblages at sea reflect the dispersion of their prey. Three hypotheses are examined which suggest that non-breeding seabirds can be used to monitor prey stocks. First, the distribution of seabirds at sea is non-random. Secondly, the distribution and abundance of seabirds correlate with aspects of the physical structure of the marine habitat. Thirdly, the basis for the consistent structures of seabird assemblages is the availability of prey.

In the Antarctic zones, very large aggregations of planktivorous seabirds (secondary consumers) dominate the avifauna. In the sub-tropical and sub-Antarctic zones, avian assemblages are characterized by a large biomass and a great diversity, due to high relative abundances of squid-eating seabirds (tertiary consumers). There is a transition zone between 47°and 50°S, where the seabird assemblages are dominated sometimes by squid-eating species and at other times by plankton-eating species. These

results of research conducted primarily in nearshore habitats (Brown, 1980; Hunt et al., 1981; Hoffman et al., 1981; Joiris, 1983; Schneider, 1983). Section 5.2 provides details on how, in deep-sea systems, meso-scale sea-surface structure influences the distribution and abundance of pelagic seabirds.

The FIBEX study (Section 5.2.1) details the non-random distribution of seabirds in a deep-sea zone which, in the macro-scale analyses, is a zone of high relative abundance. The Gough Island (Section 5.2.2) and FIBEX (Section 5.2.3) hydrographic and hydro-acoustic studies show that zooplankton and seabirds, and krill and seabirds, associate together at meso-scale sea-surface features. Unfortunately, the oceanographic data (hydrographic and hydro-acoustic parameters) collected during these cruises do not resolve sea-surface features at the scale of the significant variation in seabird abundance. Consequently, in these studies (Sections 5.2.2 and 5.2.3), regressions between the abundances of seabirds and their prey are disappointing. However, the existence of these associations can be seen in comparisons of maps of seabird abundance, the physical environment and hydro-acoustic surveys.

Section 5.2.4 presents results from the most advanced oceanographic research cruise to date in the African sector of the Southern Ocean. The Agulhas Retroflection Cruise (ARC) oceanographic data are in real-time, and a wide variety of meso-scale habitat features is resolved (Gordon, in press). The ARC study details the seabird assemblages associated with fronts, eddies, rings and currents. Moreover, the types of meso-scale oceanic processes responsible for the sea-surface structure around Gough Island and in the FIBEX sector are represented in the ARC

data (Section 5.2.4). Consequently, I am able to describe the degree to which seabird abundance correlates with a variety of meso-scale habitat features.

In the Gough Island study (Section 5.2.2), seabirds aggregate at an SST front which is similar to the meander-induced front crossed during ARC. With the appropriate scale of data, as in the ARC survey, this type of bird-SST correlation is characterized by a curvilinear regression model (Section 5.2.4). Although the correlation between seabird abundance and SST is not particularly strong in the FIBEX analysis (Section 5.2.1), both krill and seabirds are exceptionally abundant at a patch of relatively warm water (Section 5.2.3). A strong curvilinear correlation was found between seabird abundance and SST for a similar feature during ARC (i.e. a warm-core eddy). Hence, certain seabird-habitat associations are clarified by examining data sets in which environmental features are resolved at a meso-scale level of operation.

The frontal zones of the Southern Ocean are a mosaic of meso-scale sea-surface features (e.g. the 'Sub-tropical Convergence' zone) (Lutjeharms, 1981; Gordon, in press). Hulley (1981) showed that in the South Atlantic Ocean the abundance of myctophids was greatest in the vicinity of the 'Sub-tropical Convergence' zone, and Brandt (1983) and Tranter et al. (1983 a,b) showed that the diversity of zooplankton and squid aggregations were enhanced in the vicinity of eddies shed by the East Australian Current. Thus, this study pinpoints the question: Does meso-scale habitat variability enhance prey diversity, therefore producing the temporally variable, non-random distribution of seabirds observed in Section 5.2.4? The hypothesis generated by this study is that

the greater the number of meso-scale habitat-types (i.e. meso-scale features seem to be discrete habitat-types), the greater is the diversity of seabird diet-classes observed in that zone.

6.2. Seabirds as biological indicators

The hypotheses addressed in this thesis were supported sufficiently to recommend testing directly the usefulness of seabirds as indicators of the pelagic distribution of their prey. Aerial seabirds at sea in the Southern Ocean show consistent associations with the structure of their habitat. It is important to qualify this finding by discussing the limitations affecting the use of seabirds as indicators of prey distribution and abundance.

Certain species, and trophic-classes, of birds have been found to associate consistently with particular habitat conditions in terrestrial ecosystems (Landres and MacMahon, 1980; Wiens and Rotenberry, 1981; Meents et al., 1983). Wiens and Rotenberry (1981) used linear regression to examine bird-habitat relationships, which were better modelled by means of non-linear regression by Meents et al. (1983). Evidently, both marine and terrestrial birds exhibit some non-linear correlations with the structure of their habitats and, in certain cases, such correlations are strongest when local, spatio-temporal scales of data collection and analysis are considered. Apparently, lumping of data over seasons or across habitat-types or zones can mask relationsnips which exist at finer scales.

I propose that the consistent concentration of seabirds in permanent frontal zones reflects consistency in the macro-scale structure of pelagic biotic systems. If the distributions of plankton, nekton and fish are confirmed to be 'stable' on a macro-scale in the Southern Ocean (Holm-Hansen et al., 1977; Hulley, 1981; Deacon, 1982), I propose that large-scale changes in the distribution and abundance of prey stocks would be accurately reflected by changes in the macro-scale distribution of pelagic aerial seabirds. Seabird aggregations outside permanent frontal zones probably indicate relatively ephemeral occurrences of prey stocks; whereas associations between seabirds and meso-scale sea-surface features within frontal zones probably reflect more regular local concentrations of prey.

Which seabird species or diet-classes are likely to be the most useful for predicting prey concentrations in the Southern Ocean? Among the seabirds, leaving aside penguins, of each habitat area or type, there are generalist and specialist species. The generalist predator seabirds include those which take squid because they switch diets, being highly opportunistic (Croxall and Prince, 1980; Abrams, 1983). Species which take mixed-diets are by definition generalists. Planktivores and piscivores are specialists, since they require relatively frequent, specialized meals (Prince, 1980; Section 5.1.1). In terms of Levins' (1968) niche theory, specialists (i.e. narrow-niche species) show clustered distributions and generalists (i.e. broad-niche species) show more diffuse distributions; the distributions of seabirds in this study concur with Levins' (1968) contention. For example, planktivores tend to be specialists relative to squid-eating species (Croxall and Prince, 1980) and the former are more accurate indicators of sea-surface features, partially because of

their gregarious behaviour. As explained by Connell (1978: 483): "The distribution and abundance of a species are ultimately determined by tolerances to extremes of physical conditions...", it is clear that the squid-eating and mixed-diet seabirds have broad environmental tolerances in terms of their range of abiotic associations, and particularly since they apparently require food infrequently.

In low latitudes (<50° S) of the African sector of the Southern Ocean, species which are generalists in terms of foraging strategy correlate equally with permanent and ephemeral habitat features. The specialists remain as close as possible to the permanent 'Sub-tropical Front' zone or the African continental shelf. The planktivorous seabirds move to meso-scale features near to the 'Sub-tropical Front' zone, but otherwise appear to be found away from that zone only while travelling between frontal zones or breeding sites. Associations of specialist seabirds with certain features are consistent and sometimes quite strong. Generalist species are not consistently associated with specific habitat features, except that there are always some of these birds contributing to the diversity of assemblages within major frontal zones. I recommend the use of all species combined to identify macro-scale zones of prey concentration. Within such zones, particular attention should be paid to the distribution and abundance of planktivorous and piscivorous seabirds.

In the neritic ecosystem of southwestern Africa, changes in the spatio-temporal distribution and abundance of seabirds correlate with the alteration of prey stocks resulting from 30 years of commercial fishing (Crawford and Shelton, 1979; Burger and Cooper, 1984; Abrams, in press). I predict that similar changes might

occur in the deep-sea Southern Ocean avifauna, too, because its structure is probably ordered with respect to food availability and correlated with the oceanic processes which apparently control food availability. Among non-breeding seabirds of the Southern Ocean, tnere is a tendency for species which take similar diets to associate together on a macro-scale. This is convenient from the viewpoint of summarizing results because the distribution at sea of seabirds may be used by commercial fisheries for locating prey concentrations. Moreover, the proportions of planktivores increase in seabird assemblages as the predominant prey species change from squid and fish to krill along the Africa-Antarctica environmental gradient. Should krill stocks become depleted in Antarctic zones, I would expect the relative abundance of planktivorous seabirds to increase in the zones where alternative resources are available to them (e.g. zooplankton in sub-Antarctic zones).

Changes in the macro-scale availability of prey stocks to seabirds are not expected to result from changes in the marine habitat, since the macro-scale habitat structure is relatively stable. I provide information on seabird responses to short-term habitat instability, and fluctuations in the habitat of this order can be expected to influence bird populations. Therefore, alteration of the macro-scale distribution and abundance of prey stocks should be reflected in the ecological structure of the avifauna. However, the use of seabirds for ecosystem or fisheries management requires some caution. A management model would be remiss if it did not include both linear and non-linear seabird-habitat relationships. Moreover, the spatio-temporal scale of data collection and analysis must take cognizance of the distinction between macro-scale and meso-scale oceanic processes.

6.3. Conclusion

Concepts which were previously anecdotal or not quantified in a standardized fashion have been integrated in this thesis to form the basis of a hypothesis that decribes the basis for the distribution, abundance and ecological structure of deep-sea avifaunas. Although my descriptive model is a simplification of reality, it is the type of building block that can be used to direct further testing of theory (Roughgarden, 1983). My model accommodates a tendency for environmental variability since, according to Pielou (1977:109), "...theoretical equilibrium states are themselves nonstationary." Consequently, there is not a single generalized equation for the oceanographic determinants of pelagic seabird distribution. The thesis itself is a descriptive expression that sea-surface structure is the the most important mechanism affecting the organization of aerial seabirds at sea.

The field and analytical methods I use, and in some cases develop, permit the generalizations of my results to be applied and tested in other pelagic systems. However, I have also highlighted a need for exploring alternate statistical methods of developing regression models from pelagic count data which provide a high degree of predictability (e.g. generalized linear models). This thesis predicts that concurrent surveys of pelagic seabirds and their potential prey will show the following aspects of the ecological structure of pelagic seabird assemblages:

1. Seabird species diversity and biomass are greatest in the sub-tropical neritic and deep-sea frontal zones, where habitats

are most heterogeneous, and prey stocks are considered to be diverse.

2. The correlations between seabird abundance and particular hydrographic conditions are more consistent in low latitudes than in high latitudes. In low latitudes, seabird aggregations occur regularly in frontal zones, where plankton, squid or fish are considered to be relatively heterogeneous and abundant. Given improved knowledge of high-latitude oceanography, the apparently random occurrence of large seabird assemblages should correlate with ephemeral, oceanic mixing processes.

3. The variance in seabird diversity and abundance explained by regression models are more or less equal at macro- and meso-scale levels. However, within regions of high prey availability, where seabirds are likely to be foraging, the proportion of variance in bird abundance explained by regression on sea-surface temperature will be considerably higher at meso-scale than at macro-scale. Therefore, I propose that seabirds travelling between breeding and foraging areas cue principally on macro-scale environmental gradients,and, within frontal zones, seabirds which are foraging cue principally on meso-scale habitat features.

My basic contention is that pelagic avifaunas are structured ecologically along a dimension with a form largely determined by the air-sea interface and, particularly, sea-surface structure (i.e. the dispersion of water masses, currents and frontal zones). I raise the question of how the availability of some prey species to seabirds is related to these dynamic processes. Thus, I provide a hypothetical framework for testing the habitat-food-bird relationship. Moreover, I think that the consistency of the seabird-habitat correlations found throughout the extensive range

of spatio-temporal scales presented in my thesis shows that these associations provide an important reason for using seabirds as indicators of prey distribution at sea. I believe that the progress made by this study through the refinement of scale of data resolution and the introduction of non-linear statistics is sufficient to recommend continued research into the development of a model which includes seabirds as biological indicators for fisheries management.

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